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THE CELL STRUCTURE OF CLOSTERIUM EHRENBERGII AND CLOSTERIUM MONILIFERUM

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(WITH PLATES XVII AND XVIII)

Little has been contributed to our knowledge of the chromatophore and pyrenoids of Closterium since the time of NÄGELI and DEBARY, though several investigators have worked on the cell division, conjugation, and peculiar mode of locomotion of these plants.

NÄGELI (**5**) described the chromatophore, nucleus, end vacuoles, pyrenoids, and cell wall of the genus. He figures only *C. moniliferum* and *C. parvulum*, but mentions eleven other species as belonging to the genus, not including, however, *C. Ehrenbergii* among them. The chromatophore as described by him consists of three or more chlorophyll plates whose inner edges rest in the axis of the cell and whose outer edges extend to the cell wall. In optical cross section, obtained by examining the plant when it was standing on end, the chromatophore appeared to be made up of 3 to 15 plates extending radially from center to periphery. The nucleus he describes as a clear sac containing a denser body. In the colorless ends of the plant body are the clear vacuoles containing little black granules showing a motion which he calls molecular; these vacuoles are usually spherical, although at times irregular in shape. The pyrenoids, "little chlorophyll sacs," are arranged in *C. moniliferum* and *C. parvulum* in a single row of 2 to 20. The cell wall is striate. NÄGELI'S figures show, besides the external views, optical cross sections of *C. moniliferum* and *C. parvulum*. These are the only figures extant and they have been copied by OLTMANNS (**17**) and LOTSY (**12**).

DEBARY (**5**) also described Closterium, but adds little to NÄGELI'S account except that he recognizes the pyrenoids (*Amylonkerne*) as

depositing starch in their interior, and made out that the little granules in the end vacuoles are rhombic plates with sharp angles, composed, as he discovered by tests, of gypsum. DEBARY used the term *Amylonkerne* for the pyrenoids because of the many analogies they offer to the cell nuclei. He had discovered by means of the iodin reaction that the outer layer is starch, and by means of the red coloration with sugar and sulfuric acid that the central body is composed of protein. He described the starch which appears in the outer layer as either forming a homogeneous shell on the outside of this central body, or in the cells rich in starch as composed of grains that give to the pyrenoid an irregularly cracked appearance. DEBARY was the first to give an adequate account of the appearance and chemical constitution of this body in Closterium, and little of real importance as to its chemical nature has been added since.

FISCHER (**7**) examined the crystals in the end vacuoles both as to their origin and composition. In his opinion they originate in the plasma, in which he claims there are many of them, from which they wander into the vacuoles.

LÜTKEMÜLLER (**13**) and a number of other observers have studied the structure and the beautiful and characteristic markings on the cell walls of the different species.

Later authors, working on other forms, have found little to correct in DEBARY'S account of the appearance and chemical composition of pyrenoids, but DEBARY gave no adequate suggestion as to their relation to starch formation. TIMBERLAKE (**22**) has reviewed the literature fairly thoroughly, and as little has appeared since his time all that will be necessary is a brief account of the points called in question in this paper.

According to SCHMITZ (**18**), who was the first to observe and figure the process, the pyrenoid reproduces by the simple method of pinching in two, the starch mass being divided between the two daughter pyrenoids and being replaced by growth on their sides where the division had occurred. SCHMITZ'S work, which was done on Hyalotheca, has been confirmed by CHMIELEVSKY (**3**) on Spirogyra, KLEBAHN (**9**) on Cosmarium, KARSTEN (**8**) on Grammatophora, STRASBURGER (**20**) on Zygnema, and TIMBERLAKE (**21**) on Hydrodictyon. In addition to reproduction by division, it is fre-

quently assumed that they may arise *de novo* in the chromatophore, or at least arise from bodies too minute to be seen with the microscope. The apparent disappearance of the pyrenoids is characteristic of the time of spore formation and has been observed by STRASBURGER (**20**) in Cladophora, KLEBS (**11**) in Chlamydomonas and in Hydrodictyon, and OVERTON (**18**) in Volvox. They reappear when the spores begin to grow again and apparently arise *de novo*.

The commonly accepted view as to the formation of starch around the pyrenoid, as given by OLTMANNS, is that of SCHMITZ. "The origin of the starch layer out of the individual grains is very difficult to follow. If algae are taken from which the starch has been removed and put under favorable conditions for observation, there will at first appear, according to SCHMITZ, little round grains that are isolated from one another but which later grow and flatten themselves through pressure on each other." In contradistinction to this view is that of TIMBERLAKE (**21**), who found segments of the pyrenoid of Hydrodictyon breaking off and becoming converted into starch grains by the deposition of starch in each segment so cut off.

TIMBERLAKE has described many of the pyrenoids of Hydrodictyon, especially where starch formation was going on rapidly, as having two or three concentric layers of starch around them. In Cladophora (**22**) he has described the pyrenoid as a double convex lens-shaped body, from which starch grains are cut off first on one side and then on the other. These grains not being removed at once may form several layers of starch on either side. All the other pyrenoids so far described, such as those of Spirogyra, Zygnema, etc., have only a single layer of starch around them.

BÜTSCHLI (**2**) has recently made a careful study of the paramylon bodies of Euglena, and has found that in preserved material they break up into a number of disks which he regards as due to their internal structure.

The staining reactions of the pyrenoids are quite interesting and have been described by TIMBERLAKE (**21**). The pyrenoid stains a brilliant red in the triple stain, while the starch around it, and in the stroma, is colored as bright a blue.

NĚMEC (**16**) has called attention recently again to the reaction of starch to gentian violet, but uses a more complicated technique

to obtain the same result that may be had with the ordinary triple stain when properly used. He soaks his sections on the slide in a 2 per cent. aqueous solution of tannin for 10–60 minutes, washes for a minute in water, puts them into a 1.5 per cent. solution of tartar emetic for 5–15 minutes, and then stains them, after washing in water, for about 30 minutes in an aqueous solution of gentian violet. By this procedure he gets what he calls an inverse staining, in which the starch is stained a brilliant violet while the cytoplasm and chromatin remain unstained. In order to stain the chromatin he suggests a nuclear stain previously with paracarmin *in toto*. This lengthy and troublesome process is entirely unnecessary however, for the triple stain used after Flemming's fixing solutions gives sharply defined starch grains stained a brilliant blue, which is permanent for years, as our slides in use in the laboratory show, while the chromatin is a red or violet. This reaction of starch in the triple stain has been noted not only by TIMBERLAKE for pyrenoid starch, but also more recently by DENNISTON (**6**) of this laboratory for the starch of the higher plants.

Methods

While Closterium is one of the commonest of the fresh water algae in this region, it does not frequently occur so abundantly that a cytological study by means of sections can be made of it. For the past three years, however, the bottoms and sides of the lily banks in the university greenhouses, as well as the larger filamentous algae, such as Oedogonium, growing on the bottom of the tanks, have been covered during the summer months by an abundant and almost pure growth of *C. Ehrenbergii* Menegh., and during the last spring with a mixed growth of *C. Ehrenbergii* and *C. moniliferum* Ehrenb.

The Closterium was so abundant in these tanks that all that was necessary was to shake some of the plants to which they were attached in a vial of water. The Closterium would sink to the bottom and form there a layer of considerable thickness. The water could then be pipetted or decanted off and the fixing fluid added. Washing the plants and changing the alcohols and paraffins were all done in the same way, either by decantation or by pipetting off the liquid above them. About twelve hours after the change to 52° paraffin the vial was set in ice water to harden the paraffin. The vial was then broken,

the glass carefully picked away from the paraffin, and the bottom layer sectioned. I am indebted for this method to Dr. OVERTON of this laboratory, who has used it very successfully in sectioning Paramoecium.

Material was fixed in Flemming's medium, Flemming's weaker, and Flemming's weaker half strength, and Merkel's solutions. Flemming's weaker half solution strength gave the best results both on the nuclei and on the pyrenoids, causing very little shrinkage and preserving the internal structures well. With the exception of the pyrenoids, Merkel's solution preserved the cytoplasm structures better, but in the former caused shrinkage, as did the Flemming's medium solution. The sections were stained with the triple stain, the pyrenoid itself taking on a brilliant red color, while the starch around it always took the gentian stain as has already been described.

The chromatophore

As noted above, the only figures of the cross section of a chromatophore of Closterium, so far published, are those of NÄGELI, in which it is shown as composed of a central cylinder from which radiate ridges like the spokes of a wheel. In his figures NÄGELI does not show these ridges as extending to the cell wall, but in his description he says they do. The form of the chromatophore is quite different in *C. Ehrenbergii* from that described by NÄGELI for *C. parvulum* and *C. monilijerum.* In this form the central cylinder is quite large, occupying practically the entire cell space, while the ridges are comparatively narrow and extend practically to the cell wall, only an extremely thin layer of cytoplasm separating the latter from it. The chromatophore of *C. Ehrenbergii* in cross section (*fig. 2*), instead of resembling a hub with radiating spokes, as in NÄGELI's two forms, is more like a coarsely cogged wheel. The cytoplasm of the grooves between the ridges is sometimes very densely stained, being much darker than the chromatophore itself, but containing a great number of vacuoles of varying sizes (*figs. 1, 2*). At other times, however, these spaces between the ridges are almost free from stainable materials, showing only a few large vacuoles or having a very reticulate structure (*fig. 2*). When the green plants in the living condition are examined under the microscope, it can be noticed at once that there is great

variation among them; some of them are so dark green as to be almost opaque, while others are much lighter green and are semi-transparent. It is clear that the density of the cytoplasm between the ridges determines in a large degree the external appearance of the plant. DEBARY has described the chromatophore as being homogeneous, except for the pyrenoids, in surface view, but a careful examination shows that the larger vacuoles of the cytoplasm between the ridges appear as lighter areas in the darker green of the chromatophore.

The material of the chromatophore itself is in the form of a very fine reticulum, the meshes of which run out into the ridges in such a manner that in cross section the latter appear to be almost radially striate. The meshes are quite small in the outer layer of the chromatophore, but its central region shows a much coarser reticulum. The meshes here vary much in coarseness, and their structure, in connection with the cytoplasm in the grooves, determines whether the plant has a dark or light green color.

The number of ridges on the chromatophore varies from 12 to 18; this is more than is given in the systematic descriptions of this form, but it is practically impossible to count the number of ridges accurately except in sections.

Toward the ends of the Closterium the ridges seem to withdraw from the walls, and a cross section at these points shows a chromatophore with a somewhat star-shaped form and a rather thick layer of cytoplasm between the outer edges of the ridges and the cell wall (*fig. 3*). The ridges are fewer in number also, owing to the fact that some of them do not extend to the ends, and their outer edges are acute instead of blunt and rounded as is the case nearer the center.

In *C. moniliferum* (*figs. 5–7*) the structure of the chromatophore is practically the same except that the number of the ridges in my form is always 10; NÄGELI'S figures show 10 and 6. This gives an easy additional means of identifying the species in section, as the ridges of *C. Ehrenbergii* are always more numerous. The central core of the chromatophore is always larger than NÄGELI figured it. In optical cross section it gives the appearance he shows, but actual cross sections show clearly that it is essentially similar to that of *C.*

Ehrenbergii. The relative thickness of the central core as compared with the width of the ridges is shown in *fig. 4*.

The pyrenoids of *C. Ehrenbergii* are imbedded in the substance of the chromatophore close to its surface. It is very rare, except near the ends of the plant, to find a pyrenoid placed far toward the interior of the plant. In cross section it will be seen that many are either placed in the ridges of the chromatophore or lie at their bases. Although many of them lie in the ridges, none of them are found in their extreme outer edges (*fig. 2*).

Where strands of cytoplasm run across the central part of the cell body, they seem to tend to be oriented on the pyrenoids. If streaming of the cytoplasm occurs in these strands, as so frequently happens in the algae, this arrangement would put the pyrenoid in quick communication with all parts of the cell and would facilitate the movement of food products toward or away from it. It would seem to occupy a favorable position in its location so close to the surface of the chromatophore and also in its relation to other parts of the cell.

In *C. moniliferum* there is a single row of pyrenoids down the central axis. In cross section (*figs. 6, 7*) the pyrenoids occupy the center of the chromatophore. As this species is so much smaller than *C. Ehrenbergii*, there is apparently not so much necessity for the pyrenoids being at the surface.

As mentioned above, the pyrenoids in *C. Ehrenbergii* do not lie in the ridges in all cases, although many of them do. In addition to the layer of starch which incloses each pyrenoid, there are, as in Hydrodictyon, numerous starch grains lying free in the cytoplasm. These starch grains practically all lie arranged in longitudinal series in the ridges (*fig. 1*). In a longitudinal section it is rather common to see a number of pyrenoids lying in a ridge in a row, and scattered among them a number of starch grains. The grains seem to have a tendency to collect in these parts. These free grains undoubtedly had their origin around a pyrenoid, as their shape is exactly that of such grains, being angular at the edges and concave (*fig. 8*). Whether these grains became free by a second layer of starch forming around the pyrenoid and crowding out the older layer, or by the disintegration of some of the pyrenoids themselves, or in some other way,

I cannot say, but as to the common origin of both plasma starch and pyrenoid starch around some pyrenoid I can entirely confirm TIMBERLAKE'S results on Hydrodictyon. In *C. moniliferum* the stroma starch is also present and is located in the same position, at the surface of the chromatophore.

The pyrenoids

The pyrenoids of Closterium, like those of all the Conjugatae and unlike those of Hydrodictyon, as described by TIMBERLAKE, have a single layer of starch grains around them. In size the pyrenoids vary all the way from bodies almost impossible to see even with the highest magnification to spheres whose diameter is a fifteenth that of the Closterium body itself. Even the small pyrenoids have usually a little starch around them; frequently this is only on one side, but at other times it may extend all the way around (*figs. 18, 21*). These forms in which the starch occurs largely on one side are rather difficult of explanation; the one-sidedness may be due to a difference in the amount of carbohydrate food supply furnished to the two sides, or it may be due to the method of origin of the pyrenoid, as will be discussed later. A more typical form and one more frequently figured is that in which the starch lies as a mass of about uniform thickness in the form of a hollow sphere about the pyrenoid body (*figs. 10–13*). This sphere is only one layer of grains in thickness, although there were a few cases where more than one layer was suggested by the appearance of other grains just outside the regular layer. The clefts between the grains usually extend out radially, but may at times be almost tangential. The grains around any one pyrenoid vary greatly in thickness, and there are usually one or two grains of relatively larger size. The number of grains in the series around a pyrenoid is correlated with their thickness; the thicker the grains the more numerous they are and the more irregular their shape. No two pyrenoids are alike as to the shape of the grains around them. No stratification is visible either in grains or pyrenoids.

It must not be inferred that there is a correlation between the size of the pyrenoid and the thickness of the grains around it. In a general way large pyrenoids have thick grains around them (*fig. 12*), but many very small pyrenoids have thick layers of starch around

them, and some of the very largest may be without starch or have only a very thin layer. It is apparent that it is the physiological condition of the plant concerned and not the size of the pyrenoids that determines this difference. This is in harmony with the observed fact that in any one Closterium the starch layers around its pyrenoids will all tend to have the same thickness.

In fixed material, at least, the starch grains are not in direct contact with the pyrenoid. Between the body of the pyrenoid itself and the starch around it there is a layer of substance which either does not stain or stains the same color as the cytoplasm. It seems natural, of course, that there must continue to be some organic connection between the pyrenoid and the starch grains surrounding it; otherwise the starch would be moved away from its pyrenoid by the streaming of the cytoplasm, which undoubtedly occurs here in the chromatophore even if not so rapidly as it does in the cytoplasm next the cell wall. Whatever the connection may be, it must be maintained through this unstained layer, which seems from its staining reaction to be neither pyrenoid nor starch.

There is great variation in the appearance of the pyrenoid itself in different specimens. In one specimen the pyrenoids may all appear angular, while in the specimen lying next to it they are full and globular. This difference may be due to differences in the way in which the fixing solutions happen to affect the particular Closterium containing the pyrenoids, but I am inclined to think that it is rather due to some condition in the pyrenoid itself. The angular form was especially noticeable where the pyrenoids were very large and with little starch. The fixation of the general cell structure with the Flemming weak, half strength, was good in these cases, and many details in the structure of the pyrenoid could be made out. It is an interesting fact that a single cell presents in general the same type of pyrenoid throughout its whole extent.

Very few of the pyrenoids are homogeneous, although they are usually described as being so; practically all of them show parts that are denser. One of the more common forms which this dense region takes is that of an irregular star-shaped portion toward the center of the pyrenoid (*fig. 15*). In this case the central part may be very irregular, with rays extending out from it. The denser portion has

sometimes the appearance of a zone or band of darker staining material extending throughout the pyrenoid body (*fig. 22*). The ends of this zone may be split so as to give a Y-shaped figure in cross section. In a Closterium that had been fixed at night I have observed a large vacuole in the pyrenoid (*fig. 23*).

In a great number of cases the denser portions are numerous and are scattered apparently irregularly throughout the pyrenoid. A careful examination will show, however, that each dense area is opposite a starch grain, while the lighter portions are opposite the clefts between the grains, appearing merely as continuations of the latter (*figs. 10, 11*). This concentration of pyrenoid material so near to the place where starch is being laid down in the starch grain is an interesting fact, indicating that even though the rudiment of the grain may be formed as TIMBERLAKE has suggested some kind of organic connection is still retained between the young grain and the part of the pyrenoid nearest to it. The same relation might be expected to exist also if the grain is wholly a deposition product of the pyrenoid. How long this connection is retained cannot be determined. In any case, this increased concentration of the pyrenoid material in certain definite regions would seem to indicate that the pyrenoid is not a mere mass, but that it has a structure correlated more or less wholly with its function.

In many cases the pyrenoids seem to be in the process of cutting off pieces or of breaking up into a number of pieces. These may be in the form of a segment split off from one side (*figs. 16, 17*), or the entire pyrenoid may break up into lens-shaped segments (*figs. 25, 26*). Where the body of the pyrenoid itself shows a more densely staining band in cross section, these segments are cut off from one or both sides of this region (*fig. 16*). If the pyrenoid is made up of denser bodies placed opposite starch grains, the cutting off may occur along any of the lighter, less dense lines (*fig. 10*); however, hardly ever more than two of these segments are cut off and usually only one of them at any one time. The process may be traced in all its stages, from a lightly stained zone in the pyrenoid body to a small cleft, and finally to the separation of a free segment. TIMBERLAKE was able to find in the pyrenoids of Hydrodictyon that the segments changed their staining reactions from the bright red of the pyrenoid

by a series of transition stages to the violet color characteristic of the starch, but no such series of transition stages could be found in Closterium, although the segments cut off frequently appear as if stained a lighter red, owing to their smaller size. It is a question as to what becomes of these pieces of pyrenoids. Some figures seem to suggest that they round up and form smaller pyrenoids. It is very difficult to get any series of stages showing the migration of the parts away from each other, if such is the case. The hypothesis that they form other pyrenoids is supported by the fact that the starch layer is frequently of varying thickness, and may be quite thin on one side, as would happen if a segment had been cut off that side and the layer of starch had not been redeposited to any great degree (*fig. 9*).

The great variation in size of the pyrenoids is a conspicuous fact. SCHMITZ, who first observed pyrenoid division, says distinctly that they may divide equally or very unequally. It is certainly true that they are capable of splitting up into segments, whether these segments become independent pyrenoids or develop into starch grains.

In this connection the observation of BÜTSCHLI that the paramylon bodies of Euglena split up into similar shaped disks is very interesting. He regards it as due to their internal structure. The similarity of his figures to those of the pyrenoids in Closterium may indicate that paramylon bodies and pyrenoids are alike in their essential structure, even though not in chemical composition.

It should also be stated that these clefts in the body of the pyrenoid appear also in fixed and stained specimens that have not been sectioned but are examined whole.

I have observed many of the typical figures of the division of one pyrenoid to form two in material fixed at night. These figures are in all essentials like those observed by SCHMITZ in Hyalotheca and by a number of investigators since his day. It seems to consist simply in a pinching in two of the pyrenoid, and it is a curious fact that some of these same pyrenoids show the composite structure just described (*fig. 26*).

In Hydrodictyon, according to TIMBERLAKE, the pyrenoids show no such numerous clefts as are present in Closterium, and this fact makes it still more difficult to believe that the segments in Closterium

are destined to form starch grains. The origin of the starch grains and the nature and fate of the pyrenoid segments are difficult questions. That the two problems are closely related, as maintained by TIMBERLAKE, is the most suggestive conception that has so far been advanced, but the whole matter is less clear in Closterium than in Hydrodictyon. Further comparative studies on the pyrenoids of the Conjugatae will doubtless make the significance of the pyrenoid segments more clear.

A culture of Closterium was kept in the dark for three days, and then when treated with iodin showed very little starch present around the pyrenoids. Specimens from this culture were imbedded and sectioned. It was found that in most cases the starch had entirely disappeared, but that in others there were still traces of it present in the form of a thin layer around the pyrenoids (*fig. 24*). Some stroma starch was also present. The stroma starch seems to persist longer than that formed more recently around the pyrenoids. Staining the pyrenoids after keeping them in the dark was rather difficult, requiring 10–20 minutes, where before it had not taken that number of seconds; the stain was not brilliant even then. It was noticeable too that the pyrenoids had diminished one-third to one-fourth in size, showing that some of the pyrenoid substance had been used up.

The nucleus

Only a brief description of the nucleus will be given here, my principal aim at this time being to correct the erroneous view as to the shape of the chromatophore of Closterium, and to give further details as to the structure of the pyrenoids. The nucleus has in longitudinal section the form of a double convex lens (*figs. 1, 29*). Its body in both species is made up of a finely reticulate network of rather lightly staining fibers, forming meshes of almost uniform size. There seem to be no differentially stained chromatin granules on the strands. There are darker masses in the fibers which may be the net knots of the older authors; the extreme fineness of the network makes this point especially difficult to determine. The most striking part of the nucleus is the great mass of granules which lie in a group in the center of this reticulum and which stain a brilliant red in the triple stain. These bodies are globular or sometimes somewhat angular granules of varying size, apparently unconnected and lying free

in the reticulum. The strands from the fine-meshed reticulum surrounding them seem to come up to these granules and apparently hold them in position. These granules in *C. Ehrenbergii* are usually arranged in a fairly compact mass of varying size at the center of the nucleus (*fig. 1*), but they may be scattered out in an irregular manner across the long axis of the nucleus (*fig. 29*). In *C. moniliferum* (*fig. 28*) these bodies form a mass that is practically spherical, but shows a few irregularities on its surface. The nucleus in this species resembles that of Spirogyra very much, but it can be made out that the central spherical mass is made up of smaller pieces, while in Spirogyra the so-called nucleole appears as a homogeneous sphere.

The real significance of these granules and of the meshwork that surrounds them, and the part which each takes in cell division, can be determined only by seeing them during the time of chromosome formation. Their behavior will throw light on the nature of the so-called chromatin nucleolus of Spirogyra, in which, as described by MITZKEWITSCH (**14**), BERGH (**1**), and others, is contained all the chromatin in the nucleus. I shall discuss the phenomena of nuclear and cell division in a further paper.

My indebtedness to Professor R. A. HARPER for his advice and criticism during the progress of this work is very great, and I take this opportunity of expressing my appreciation of them.

Summary

1. The current figures and descriptions of the chromatophore of Closterium derived from NÄGELI are fundamentally incorrect. The chromatophore is not made up of a series of radiating plates about a slender central core, but is a curved cone-shaped structure with relatively narrow ridges on its surface.

2. The pyrenoids are imbedded in the periphery of this chromatophore in *C. Ehrenbergii* and exactly at its center in *C. moniliferum*.

3. Pyrenoid starch and stroma starch both have the same origin, all the starch being formed around pyrenoids.

4. The pyrenoids show considerable internal structure, frequently containing denser and lighter portions, vacuoles, etc., and often are cleft into a mass of disks or segments of varying number and form.

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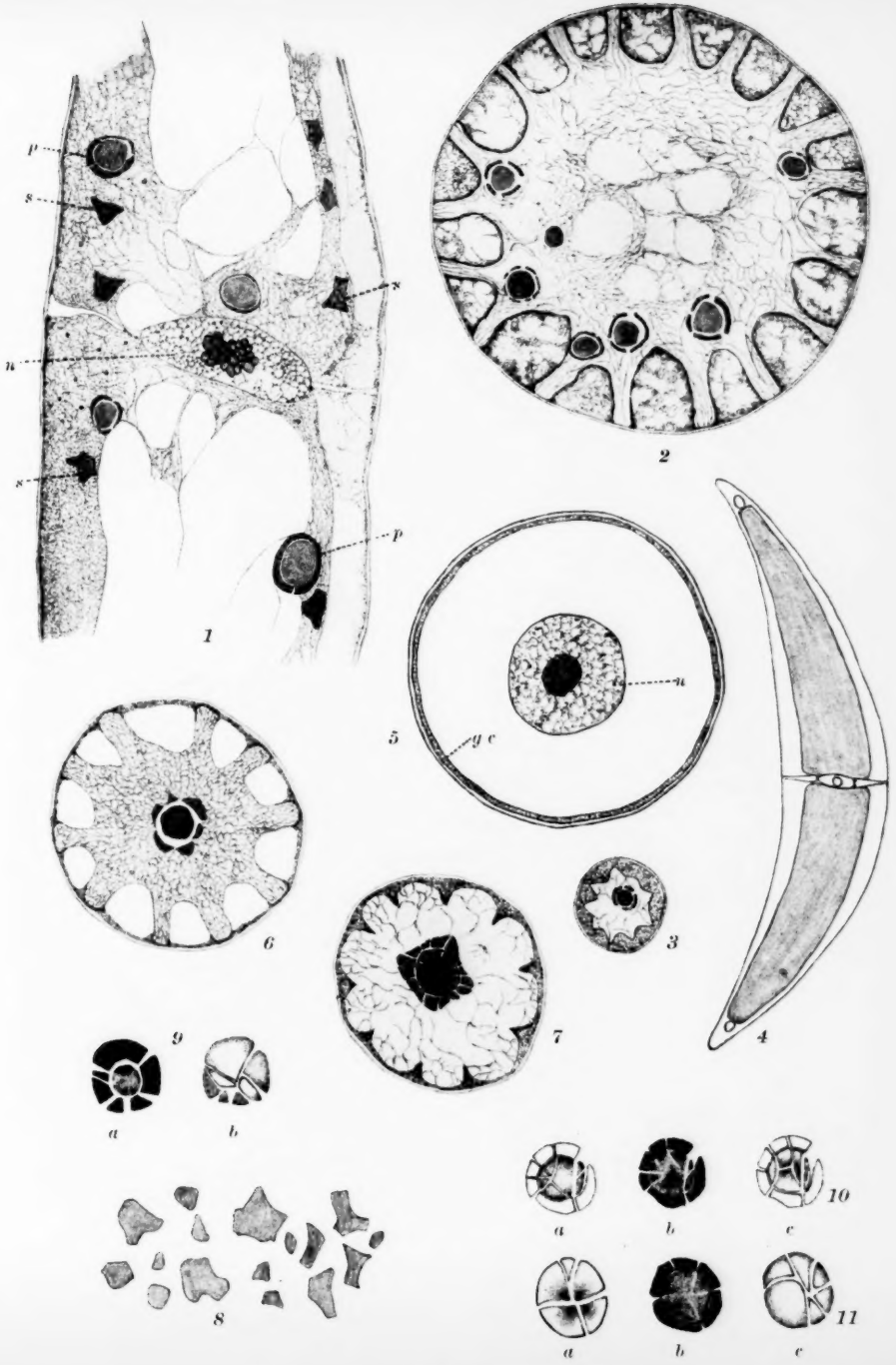

LUTMAN on CLOSTERIUM

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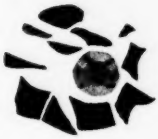

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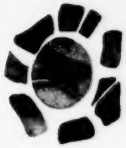

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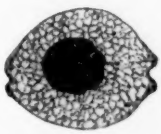

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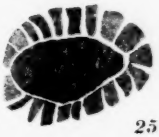

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HELIOTYPE CO., BOSTON.

EXPLANATION OF PLATES XVII AND XVIII

MAGNIFICATION.—*Figs. 1, 2, 5, 6, 7,* about ×900; all the others, about ×1250.

FIG. 1.—*C. Ehrenbergii;* longitudinal section; on the left the section is through one of the ridges; on the right it is through one of the furrows; *n*, nucleus; *p*, pyrenoids; *s*, stroma starch.

FIG. 2.—*C. Ehrenbergii;* cross section.

FIG. 3.—*C. Ehrenbergii;* cross section near one end, showing star-shaped chromatophore.

FIG. 4.—*C. moniliferum;* shaded portion is the central part of the chromatophore.

FIG. 5.—*C. moniliferum;* schematic cross section through the nucleus (*n*); *gc*, granular cytoplasm.

FIG. 6.—*C. moniliferum;* cross section about half-way to the tip.

FIG. 7.—*C. moniliferum;* cross section nearer the tip.

FIGS. 8–26.—*C. Ehrenbergii;* details of starch and pyrenoids.

FIG. 8.—Stroma starch.

FIG. 9.—Pyrenoid showing internal markings; *a*, in section; *b*, surface view of the starch mass.

FIG. 10.—Pyrenoid showing internal markings; *a*, section of starch showing top of pyrenoid; *b*, section of starch and pyrenoid; *c*, section showing lower part of the starch.

FIG. 11.—Pyrenoid; *a*, section; *b*, top surface of starch mass; *c*, bottom of same.

FIGS. 12, 13.—Pyrenoids; *a*, surface view of starch; *b*, section of pyrenoid.

FIG. 14.—Pyrenoid; *a*, section; *b*, surface view of starch; *c*, view of the starch at deeper level.

FIG. 15.—Pyrenoid; *a*, surface of starch; *b*, section of pyrenoid.

FIGS. 16–22.—Pyrenoids showing pieces cut off.

FIG. 23.—Pyrenoid with large vacuole.

FIG. 24.—Pyrenoid after Closterium has been kept in the darkness for three days.

FIGS. 25, 26.—Pyrenoids showing peculiar disks into which the pyrenoid body has broken up.

FIG. 27.—Pyrenoid as ordinarily figured in division.

FIG. 28.—Nucleus of *C. moniliferum*.

FIG. 29.—Nucleus of *C. Ehrenbergii*.

CLIMATOLOGY AND VEGETATION IN COLORADO

W. W. Robbins

(WITH SEVEN FIGURES)

To the student of botany, it matters not in what part of the United States he lives or in what branch of botanical work he is engaged, the state of Colorado is an interesting and attractive area. The general inland location of the state, great differences of altitude, of latitude, and of topography, are factors which bring about varied climatic conditions, resulting in corresponding vegetative differences. It is the purpose of this paper to give a general view of the climatological conditions of Colorado in their relation to vegetation. The necessity of pointing out in ecological and phytogeographical studies the relation between the climatology of an area, extended or restricted in its range, and the vegetative covering, is being increasingly recognized. The climatologist and the field botanist must join hands. Not only is the botanist coming to realize his dependence upon a thorough knowledge of climatology as a basis for his phytogeographical studies, but in a like manner is the climatologist coming to see that the distribution of the indigenous vegetation will aid him. This fact has been recognized by the Maryland Weather Service, which has undertaken a botanical survey of that state as a part of its climatic studies.

Physiography and climatology

PHYSIOGRAPHY

Topography.—The general topographic features of the state are given in *fig. 1*. The eastern half of the state is plains. This region is limited on the west by the foothills, which extend from the northern to the southern borders of the state, following closely the 6000-foot contour line. The foothills rise one over the other, extending westward to the main range. The continental divide passes irregularly in a north and south direction through the state. It is therefore a barrier to the east and west distribution of plants. In the mountainous region there are four large parks or high valleys: North, Middle, South, and San Luis parks. They are broad, level expanses of

country having an elevation of 6000–10,000 feet and inclosed by high mountains; hence they are very dry and the vegetation is more xerophytic than that growing at the same altitudes in uninclosed areas. There are parts of western Colorado, however, where xerophytic conditions exist at high altitudes, the dryness in this case being due to the unequal seasonal distribution of precipitation. Western Colorado is for the most part high; high, flat tablelands and mesas,

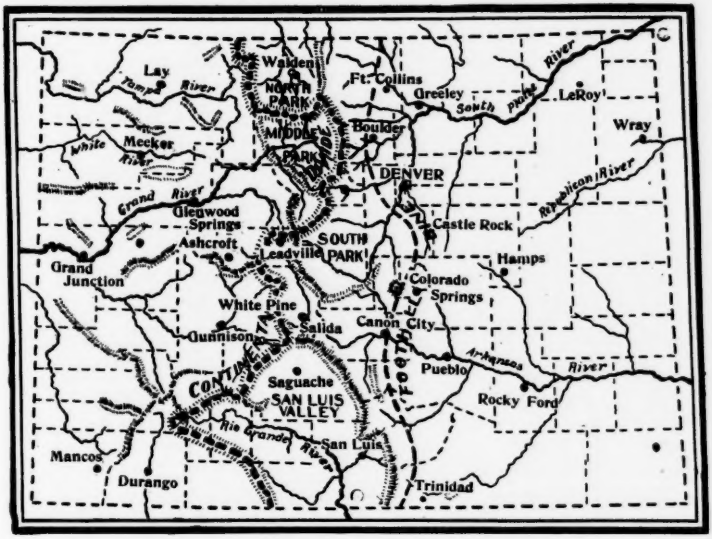

FIG. 1.—General topographic features of the state; east of the foothill line lie the great plains.

dissected by narrow steep canyons, are characteristic. Many of the minor mountain ranges have an east and west trend.

An important topographic feature of the eastern part of the state is the Arkansas-Platte Divide, extending plainward from the foothills in the middle of the state. Foothill forms of vegetation have an eastward extension on this divide. It also marks the northern and southern limit of some species, such as the pinyon pine (*Pinus edulis* Engelm.), the chandelier cactus (*Opuntia arborescens* Engelm.), and *Populus Wislizenii* (S. Wats.) Sarg., which do not occur north of

the divide. The same is true to a less extent of the scrub oak; on the eastern slope this plant is not abundant north of the Arkansas-Platte Divide.

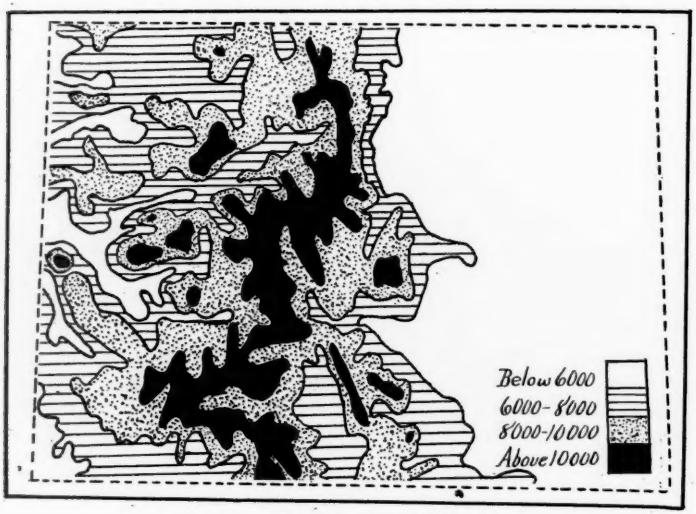

FIG. 2.—Mass elevations of Colorado.

ELEVATION.—Colorado has an area of 103,480 square miles.[1] The following table gives the mass elevations of the state in area and percentages.

TABLE I

MASS ELEVATIONS

Elevation	Area in sq. miles	Percentage of total area
6000 feet and below	45,000	43
6000–8000 feet	22,000	20
8000–10,000 feet	24,000	23
10,000 feet and above.....	12,500	14

From the above table and the accompanying map showing mass elevations (*fig. 2*), it is seen that a great proportion of the state is highly

[1] GANNETT, HENRY, Report U. S. Geol. and Geog. Survey of the Territories (Hayden Survey) 313. 1876.

mountainous. The lowest point in the state has an elevation of 3386 feet; there are a number of peaks over 14,000 feet high; thus there is an altitudinal range considerably over 11,500 feet.

DRAINAGE SYSTEMS.—The general north and south direction of the mountains of Colorado determines the general east and west direction of the streams. In the mountainous country small streams are very

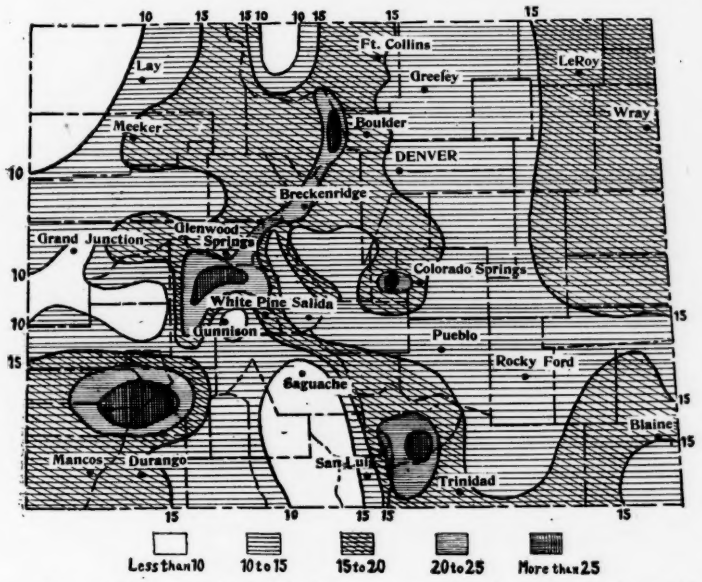

FIG. 3.—Mean annual precipitation: the area along the eastern border of the state having 15–20 inches annually is called the "rainbelt"; dry farming is more successful here than in the belt on the west of it.

abundant, and they usually have their head in a wet mountain meadow which is fed by water from melting snow. The prevalent east and west direction of the streams is a condition affecting the migration of riparian species. Generally speaking, the streamside flora and vegetation at any point is more like that east and west than that north and south.

PRECIPITATION

GENERAL ACCOUNT.—The precipitation amounts of Colorado are shown in *fig. 3*. In making a rainfall map it is found difficult to

depend upon rain gauge records alone, because of the variety of conditions at intermediate points which are brought about by topographical conditions. Hence in preparing this map, as well as the ones of temperature, the influence of the larger topographic features and of altitude have been taken into consideration. Fortunately,

TABLE II

SEASONAL DISTRIBUTION OF PRECIPITATION EAST AND WEST OF DIVIDE

STATION	ALT. (FEET)	EAST OF CONTINENTAL DIVIDE			WEST OF CONTINENTAL DIVIDE		
		Mean for growing season	Mean for year	Perc'tage during growing season	Mean for growing season	Mean for year	Perc'tage during growing season
Ashcroft	9483	.....	.....	..	10.67	19.38	55
Blaine	3935	12.36	16.08	77			
Boulder	5347	12.83	18.46	69			
Breckenridge	9536	.....	.....	..	11.99	26.76	72
Castle Rock	6220	12.73	17.65	72			
Cheyenne	6088	9.40	12.20	77			
Collbran	6000	.....	.....	..	7.33	14.59	50
Colorado Springs	6098	13.00	14.41	90			
Denver	5272	10.03	14.02	72			
Durango	6534	.....	.....	..	8.25	16.62	50
Ft. Collins	4985	11.06	14.91	73			
Grand Junction	4608	.....	.....	..	4.27	8.50	50
Hamps	5400	11.82	14.56	81			
Holly	3386	12.71	15.32	71			
Idaho Springs	7543	10.65	15.44	68			
Lake Moraine	10625	18.44	25.59	72			
Lay	6162	.....	.....	..	6.37	12.72	50
LeRoy	4380	12.22	16.05	76			
Mancos	6960	.....	.....	..	9.29	17.29	53
Meeker	6182	.....	.....	..	8.42	15.91	53
Pike's Peak	14108	19.07	28.65	66			
Pueblo	4734	9.17	12.11	75			
Saguache	7745	5.45	7.21	75			
Salida	7035	7.62	11.47	67			
Wray	3512	14.57	18.11	80			
Mean average		11.84	15.90	**74**	8.57	16.45	**52**

however, the meteorological stations in Colorado are numerous enough and so happily distributed, that one is able to rely upon them as being fairly representative.

The eastern part of the state has more rain (15–20 inches) than a strip closer to the mountains (10–15 inches). On the eastern slope of the mountains, localities between 6000 and 10,000 feet altitude have an annual precipitation of 15–20 inches; many localities have

greater amounts. The higher mountainous parts receive over 20 inches annually. North, Middle, and San Luis parks are very dry, the annual precipitation being less than 10 inches; South Park is drier than localities at the same altitude on the eastern slope. On the western slope there is a gradual decrease westward in the annual rainfall, which becomes on the western border less than 10 inches.

SEASONAL DISTRIBUTION.—The precipitation of Colorado shows great variability, not only in amount but also in seasonal distribution.

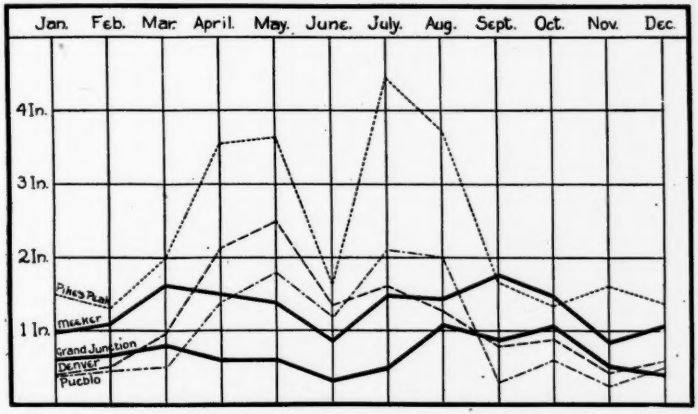

FIG. 4.—Mean annual precipitation curves: Meeker (6182 feet) and Grand Junction (4594 feet) are west of the continental divide; Pike's Peak (14,108 feet), Denver (5275 feet), and Pueblo (4672 feet) are east of the continental divide; the curves for Meeker and Grand Junction in heavy lines are very regular, showing an equal distribution of precipitation throughout the year; on the other hand, the curves for Denver, Pike's Peak, and Pueblo show for those stations a very unequal seasonal distribution; the season of maximum rainfall for each station will be noted.

From table II and *fig. 4*, it is seen that at stations east of the continental divide the greater part (average 74 per cent.) of the precipitation occurs during the growing season, when vegetation needs it, and this usually in the months of April, May, and June. On the other hand, west of the continental divide only about one-half (average 52 per cent.) occurs during the growing season, the most rainy months being July, August, and September. For this reason, so far as plant life is concerned, localities on the western slope are drier than localities at

the same altitudes on the eastern slope. The precipitation of Colorado comes in showers rather than in prolonged rainy spells.

There is considerable variability as to the wettest part of the growing season. In the region north of the Arkansas-Platte Divide, the rainy months are April and May, with the exception of localities over the extreme eastern part of the state, where the maximum rainfall occurs in June. Consequently, the vernal vegetation of this region is more luxuriant than one would judge from the annual precipitation; the rest of the season is dry and is marked by the blooming of xerophytic species, mainly composites. The Arkansas-Platte Divide and the entire Arkansas Valley receive their maximum rainfall during the summer, July showing the greatest monthly amount. In the mountains July and August are the wettest months. Over the western slope the spring is wetter than the other seasons, but July or August generally shows the greatest monthly precipitation.

On account of the seasonal distribution of precipitation east of the continental divide there is very little snow. Furthermore, on account of the dry soil and air the snow soon disappears after falling. This is especially true of the plains, and as a result the vegetation does not have during the winter the protection which snow offers. The absence of snow on the plains, with the consequent low soil-moisture content, the great diurnal and annual ranges of temperature, together with the presence of a low relative humidity and dry winds, bring about conditions which account for the absence of trees.

As a result of the shortness of the rainy season, at most localities on the plains and lower foothills there is an acceleration in the growth of vegetation. Seasonal rains are usually followed by drought periods, and mesophytic plants must hasten to complete their development; hence the vegetative appearance changes rapidly.

Very wet and very dry years, or a consecutive series of these, are not uncommon in Colorado. The mean difference between the wettest and driest years is somewhat greater for localities east of the continental divide than for localities west. Plants living in a place where there are occasional very dry and very wet years must be those that have adapted themselves more or less successfully, not only to the normal precipitation, but to the variability of the same.

INCREASE OF PRECIPITATION WITH INCREASE OF ALTITUDE.[2]—It may be stated as a general rule that rainfall increases in amount and frequency with an increase in altitude. There are numerous exceptions which are due to topography. It has been pointed out by HANN (*l. c.* 305) that high mountains possess a zone of maximum precipitation above which there is a decrease. So far as the records for high altitudes in Colorado go, they indicate no such maximum zone, there being an increase to the summits.

It is well known that the increase in the amount and frequency of the precipitation in passing from lower to higher altitudes has its influence upon the vegetation. This influence finds its best expression in the arborescent vegetation. The forests on the lower slopes of the mountains are chiefly xerophytic, while those of the higher altitudes are predominantly mesophytic.

Table III gives an idea of the rate of increase of precipitation with an increase of altitude as it occurs in Colorado. Hence it indicates as well the frequency of vegetational changes, which are due in the main to precipitation amounts.

TABLE III

RATE OF INCREASE OF PRECIPITATION WITH INCREASE OF ALTITUDE

Station	Altitude (feet)	Precipitation (inches)	Number of feet increase in altitude giving increase of one inch of precipitation
Colorado Springs	6046	14.41	377
Lake Moraine	10246	25.59	1272
Pike's Peak	14108	28.65	
Denver	5272	14.02	1599
Idaho Springs	7543	15.44	
Gunnison*	7670	9.19	269
White Pine*	9500	16.00	
Glenwood Springs*	5823	13.20	592
Ashcroft*	9483	19.38	

* West of continental divide.

From the above table it will be seen that the rate of increase of precipitation is less at higher altitudes than at lower; also that on the western slope the rate of increase is more rapid than on the eastern slope.

[2] HANN, Handbook of climatology, p. 301.

TEMPERATURE

GENERAL ACCOUNT.—*Fig. 5* shows the mean annual temperatures of Colorado. The general north-south direction of the isotherms readily shows the influence of the mountains. The eastern portion of the state and a small area along the Grand River in the western part have a mean annual temperature above 50° F.[3] The influence

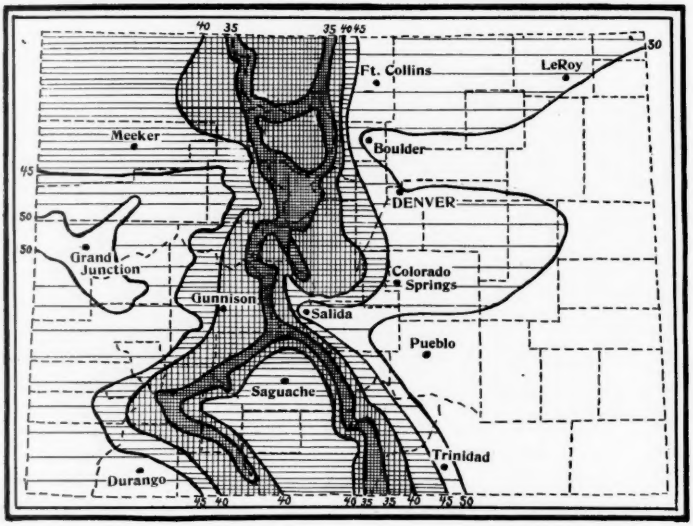

FIG. 5.—Mean annual temperatures: the general appearance of this figure is very similar to the one giving mean summer temperatures (*fig. 6*), and to the one showing mass elevations (*fig. 2*).

of the Arkansas-Platte Divide is seen in the eastward deflection of the isotherm 50. Isotherm 45 follows closely the eastern foothill line, 6000 feet altitude; it indicates the lower limit of the Rocky Mountain yellow pine (*Pinus scopulorum* [Engelm.] Lemmon). Isotherm 40 follows closely the 8000-foot contour line, and marks the lower limit of the lodgepole pine (*Pinus Murrayana* Oreg. Com.) and the usual upper limit of the Rocky Mountain yellow pine. On the western slope these isotherms run to higher altitudes. There is a decrease in the temperature with an increase in altitude, most localities

[3] Throughout this paper all temperature readings are Fahrenheit.

above 10,000 feet having a mean annual temperature below 35°. Isotherm 35 follows approximately the upper limit of lodgepole pine, separating the montane from the subalpine zone. The mean autumn and spring temperatures are very nearly the same as the annual mean. As a rule, the fall mean is somewhat higher and the spring mean lower than the annual mean. *Fig. 6* gives the mean summer temperatures

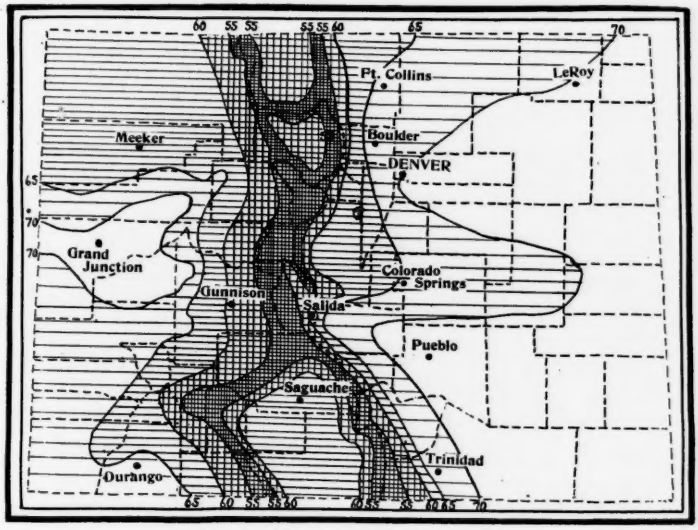

FIG. 6.—Mean summer temperatures.

of Colorado. Its general appearance is similar to the mean annual temperature map. On the eastern slope isotherm 65 marks the lower limit of the foothill zone. Isotherm 60 on both slopes follows the lower limit of the montane zone and isotherm 55 the lower limit of the subalpine zone. No data are at hand to show the temperature conditions at timber line.

RANGE OF TEMPERATURE.[4]—For the state as a whole the mean annual range (difference between the mean temperature for the warmest month and mean temperature for coldest month) is great (see table IV). In the Arkansas Valley, Platte Valley, Grand Valley,

[4] HANN, *l. c.*, p. 273.

and northwestern part of the state the mean annual range is greatest. There is a decrease in the range with an increase of altitude. The annual march of temperature for typical localities is shown in *fig. 7*. For most stations in the state January is the coldest month, July the warmest.

TABLE IV

MEAN ANNUAL RANGE OF TEMPERATURE

Locality	Coldest month	Mean temperature	Warmest month	Mean temperature	Mean annual range
Blaine	February	31.6	July	76.2	44.6
Boulder	February	30.7	August	70.7	40.0
Breckenridge	January	15.4	August	53.5	38.1
Cañon City	January	33.7	July	73.0	39.3
Castle Rock	January	26.6	July	68.3	41.7
Cheyenne	January	25.6	July	67.4	41.8
Collbran	January	22.0	July	68.8	46.8
Colorado Springs	January	27.5	July	68.0	40.5
Cope	February	27.4	August	74.9	47.5
Denver	January	29.1	July	71.8	42.7
Durango	January	24.5	July	68.7	44.2
Fort Collins	February	26.1	July	68.5	42.4
Fort Morgan	January	25.0	July	72.8	47.8
Garnett	January	14.2	July	61.1	46.9
Grand Junction	January	24.7	July	79.2	54.5
Grand Valley	January	23.9	July	72.9	49.0
Gunnison	January	7.3	July	60.9	53.6
Hamps	February	26.1	July	67.1	41.0
Hoehne	January	29.9	July	70.5	40.6
Idaho Springs	January	27.4	July	62.2	34.8
Lake Moraine	February	20.4	August	53.5	33.1
Lamar	January	31.4	July	77.5	46.1
Las Animas	January	26.4	July	76.9	50.5
Lay	January	18.1	July	67.3	49.2
LeRoy	February	25.4	August	71.5	46.1
Mancos	January	26.3	July	66.0	39.7
Meeker	January	19.6	July	65.9	46.3
Pagoda	January	19.4	July	63.9	44.5
Pueblo	January	29.1	July	74.2	45.1
Rangely	January	13.9	July	70.2	56.3
Rocky Ford	January	28.9	July	74.3	45.4
Salida	January	27.7	July	64.9	37.2
San Luis	January	19.8	July	62.8	43.0
West Cliffe	January	24.3	July	61.1	36.8
Wray	February	28.9	July	73.7	44.8

The diurnal range of temperature is great over the entire state. This is especially so on the plains, in the western part of the state, and in the parks. It is least in the higher mountain regions.

The high annual and diurnal ranges of temperature on the plains and other treeless areas of the state must receive no little consideration

in explanation of the cause of the treeless condition. For example, the Rocky Mountain yellow pine will grow on the plains without irrigation if it is tided through the seedling stage. The seedling cannot tolerate great extremes of temperature.

DECREASE OF TEMPERATURE WITH INCREASE OF ALTITUDE.[5]—The rate of decrease varies with the topography, altitude, and season. It

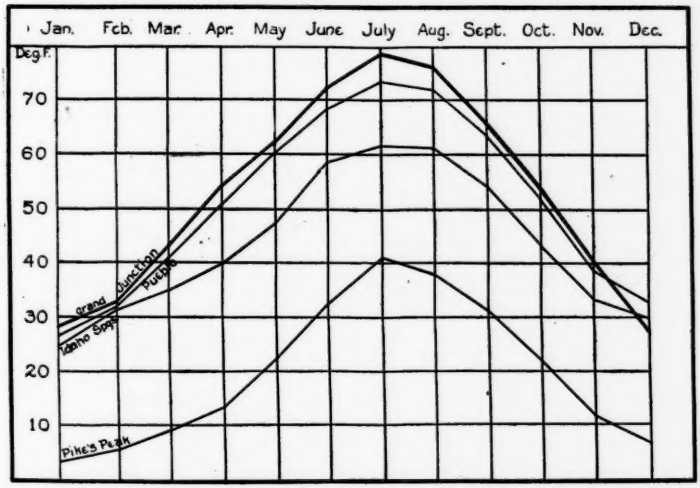

FIG. 7.—Mean annual march of temperatures: Grand Junction (4594 feet) in the western part of Colorado and Pueblo (4672 feet) on the plains have a much smaller range of temperature than do the mountain stations Idaho Springs (7453 feet) and Pike's Peak (14,108 feet).

is less at high altitudes than at lower and less in winter than in summer. Table V gives the decrease in temperature for an increase in altitude for several Colorado stations.

Colorado Springs is at the base of Pike's Peak; Lake Moraine is at an elevation of 10,265 feet on its eastern slope. It will be seen from the table that the decrease of temperature between Lake Moraine and Colorado Springs is less than that between Lake Moraine and Pike's Peak. This is contrary to the general rule, and is probably due to the inversion of temperature which occurs at the base of the moun-

[5] HANN, *l. c.*, p. 243.

tain, bringing the mean temperature of Colorado Springs lower than it would be if inversion did not take place. The data for the last three sets of localities in the table are for one season only.

TABLE V

DECREASE IN TEMPERATURE WITH INCREASE OF ALTITUDE

Stations compared	Decrease of temperature per 1000 feet (in degrees F.)
Pike's Peak–Colorado Springs*	3.4
Pike's Peak–Lake Moraine*	4.3
Lake Moraine–Colorado Springs*	2.6
Boulder–Arapahoe Peak at timber line†	3.2
Denver-Corona*	3.6
Boulder–Redrock Lake‡	3.2

* Data from Annual Summary of Colorado Division of the Climatological Service.

† Data from YOUNG, ROBERT T., Forest formations of Boulder County, Colorado. BOT. GAZETTE 46:321–352. 1907.

‡ Data from RAMALEY, FRANCIS, AND ROBBINS, W. W., Studies in lake and streamside vegetation. 1. Redrock Lake near Ward, Colorado. Univ. Colo. Studies 6:133–168. 1909.

INVERSION OF TEMPERATURE.[6]—This phenomenon is common in mountainous regions, being particularly noticeable in the spring and autumn. The valleys and canyon bottoms are often cooler than the adjacent hillsides; the plains are cooler and have greater diurnal range of temperature than the overhanging foothills.[7]

A comparative study of temperatures of the University of Colorado campus[8] and the mesas near by, 415 feet higher, showed for May 1908 the mean monthly difference in temperature to be 2°.6 higher on the mesas than on the campus. Furthermore, the last frost in the spring was 16 days later on the campus than on the mesa. This inversion is undoubtedly present all along the foothills. Mesas have a milder climate than adjacent plains, and the early spring vegetation is in advance of that on the plains. On account of temperature inversion in canyons and gulches, high altitude forms find their lower

[6] HANN, *l. c.*, p. 252.

[7] In the southern Alleghenies, CHICKERING (J. W., JR., Thermal belts. *Amer. Meteor. Jour.* 1: 213–218. 1884–85), quoting SILAS MCDOWELL of Franklin, Macon County, N. C., describes the presence there of a "thermal belt" or "frostless zone" upon the mountain sides, commencing at about 300 feet vertical height above the valley and having a breadth of 400 feet vertical height.

[8] RAMALEY, FRANCIS, Climatology of the mesas near Boulder, Colo., in Studies on mesa and foothill vegetation. Univ. Colo. Studies 6:11–49. 1909.

limit of distribution in gulches rather than on ridges, and low altitude forms extend farther up the ridges than up the gulches.

At certain periods, inversion of temperature of more than local influence occurs along the eastern edge of the foothills, which up to a considerable altitude experience a higher temperature than the plains. LOUD[9] points out that on the eastern slope of the Rocky Mountains in Colorado he has often noticed that elevated stations retain a mild temperature for some time after a cold wave has set in at a lower level.

There is much need of thorough investigation of the amount of temperature inversion for various localities; of determining its limits, time of occurrence, and effect upon the vegetation. There is little doubt that an investigation of such a nature would reveal information of practical importance to horticulturists and throw light on problems of plant distribution.

FROST.—The average date of the last killing frost in spring, of the first killing frost in autumn, and the average length of the growing season (period without frost) are important climatic factors. In Colorado these factors are affected to a considerable degree by temperature inversion, and have a great range on account of altitudinal differences. Grand Junction has the longest growing season of any locality in the state (6 months and 18 days), while on the highest peaks there is no day in the year without frost.

TABLE VI

EFFECT OF ALTITUDE UPON AVERAGE LENGTH OF GROWING SEASON AND AVERAGE DATE OF LAST KILLING FROST

Altitude (feet)	Average date of last killing frost	Average length of growing season (period without frost)
5000 and below	April 28	5 months, 6 days
5000–6000.....	May 5	4 months, 21 days
6000–7000.....	May 30	3 months, 21 days
7000–8000.....	June 6	3 months, 6 days

There are no data for higher altitudes. During the summer of 1908, the length of the growing season at Redrock Lake, altitude 10,100 feet, was about 6 weeks. Table VI shows that the retardation in the development of vegetation is about 13 days for every 1000 feet increase in altitude.

[9] LOUD, F. H., The Colorado sky 1:1–9. 1908.

HUMIDITY

Unfortunately very little information regarding the relative humidity of different parts of Colorado is to be had. The state as a whole, however, has a low relative humidity. Along the eastern border of the state the mean annual relative humidity is about 60 per cent.; east of the foothills the mean annual amount is 48–50 per cent.; in the extreme western part of the state the annual relative humidity is 46–50 per cent. In the mountains there are rapid variations and great extremes of relative humidity.[10] The following from HANN (*l. c.* 289) gives the seasonal march of relative humidity on Pike's Peak, altitude 14,147 feet: winter, 79 per cent.; spring, 81 per cent.; summer, 75 per cent.; autumn, 77 per cent.; year, 78 per cent. Over the entire state, the relative humidity is greatest in the winter. Because of low relative humidity thin-leaved plants are almost unknown in the state, only a very few being able to maintain themselves in the densest shade of steep-walled canyons.

WIND

On the western slope the average wind velocity is 5–6 miles per hour; on the eastern slope 7–7.5 miles per hour; on the northern and eastern borders 10 miles per hour. In the higher mountains, especially on exposed ridges and peaks, the wind has a great velocity and blows almost steadily the year round. Here the winters are extremely windy. Over the whole state, the prevailing direction of the wind is from the west. Along the eastern base of the mountains there occur, during the winter and early spring, warm west winds, called "chinooks." These cause the sap to flow and the buds to swell, only to be followed by a low temperature which proves destructive to vegetation. Mountain and valley winds, which during the day blow up the valleys and at night toward the plains, bring about diurnal variations of humidity, cloudiness, and precipitation. As a result of the day direction of the winds, the mountains are often visited by afternoon showers.

[10] I am informed by Professor FRANCIS RAMALEY that records of relative humidity made at Tolland, Colorado, altitude 8889 feet, during the summer of 1909, do not show as great fluctuations as is usually expected in mountain regions.

SUNSHINE AND CLOUDINESS

Colorado is a state of sunshine. On the average, 50 per cent. of the days are clear, 33 per cent. partly cloudy, and 17 per cent. cloudy.

Vegetation

PLAINS[11]

Precipitation: mean annual 10–20 inches; about 75 per cent. during the growing season; small amount of snow. *Temperature:* mean annual 45°–50° and above; mean summer 65°–70° and above; mean annual range 40°–50°; diurnal range great. Average date of the last spring frost varies in different localities from April 28 to May 10; average length of growing season about 5 months, 6 days. *Relative humidity:* annual amount 50–60 per cent.

The plains are generally spoken of as including that portion of the state east of the foothills. The climatic and vegetative conditions vary, however, in different parts. The "high plains"[12] north of the South Platte River, the Arkansas-Platte Divide, and the high lands east of the foothills in the southern part of the state are regions over which foothill forms have extended. It will be observed from *figs. 5* and *6* that these areas have a lower mean annual temperature (45°–50°) and a lower mean summer temperature (65°–70°), with a consequent less evaporation rate than the plains proper.

Over the entire plains area grasses are the dominant forms of vegetation; in some places not more than 25 per cent. of the ground is covered. Some of the common grasses are *Andropogon Hallii* Hack., *Calamovilfa longifolia* (Hook.) Hack., *Bouteloua oligostachya* (Nutt.) Torr., and *Bulbilis dactyloides* (Nutt.) Raf. *Eurotia lanata* (Pursh) Moq., *Sarcobatus vermiculatus* (Hook.) Torr., and *Chrysothamnus graveolens* (Nutt.) Greene are abundant in many localities. On ridges and buttes occur various shrubs, such as *Yucca glauca* Nutt., *Prunus Besseyi* Bailey, and *Ceanothus pubescens* (T. and G.) Rydb., also various mat and rosette-forming herbs. *Populus angustifolia* James, *P. Sargentii* Dode, *P. acuminata* Rydb., *P. Wislizenii* (S.

[11] The classification of the plant zones into plains, foothill, montane, subalpine, and alpine are as outlined by RAMALEY, FRANCIS, Plant zones in the Rocky Mountains of Colorado. Science N. S. **26**:642, 643. (Nov. 8) 1907.

[12] RAMALEY, FRANCIS, Scientific expedition to northeastern Colorado; 8. Botany. Account of collections made. Univ. Colo. Studies **4**:161–164. 1907. This report gives a list of plants characteristic of the "high plains."

Wats.) Sarg., and *Salix* spp. fringe the streams. East of the continental divide, *P. Wislizenii* occurs only in the southern part of Colorado.[13] *Opuntia arborescens*, the chandelier cactus, extends over large areas in the Arkansas Valley; this plant is also restricted in its distribution on the plains to the southern part of the state.

In their *Phytogeography of Nebraska*, POUND and CLEMENTS have divided that state into four regions, two of which, the sand-hill region and the foothill region, extend into Colorado. The sand-hill region in Colorado includes a narrow strip along the eastern part of the state. Their "foothill region," so called because of the great number of mountain plants which here find their eastward distributional limit, occupies the rest of the plains area. In describing the general appearance of the sand-hill region, they say: "The most noticeable character of the sand-hill vegetation, after one has become accustomed to the great variety of species which the sparse vegetation of each hill affords, is its extreme monotony. This is due to the predominance of bunch grasses, which are the controlling element in the covering of the hills, hillsides, sandy ridges, and sandy tablelands of the water sheds. The principal formation of the sand-hills, then, is the bunch grass formation, a grass formation of exposed hills and ridges of pure sand."

EASTERN LOWER FOOTHILLS AND MESAS[14]

Precipitation: mean annual 15–20 inches; about 75 per cent. during the growing season; in the northern part of the state the early spring is the wettest season, in the southern part July and August are the wettest months; more snow than on the plains. *Temperature:* mean annual 45°–50°; mean summer 65°–70°; mean annual and diurnal ranges less than on the plains. Average date of last spring frost April 27 to June 16. As a result of temperature inver-

[13] The writer recently found a few trees of this species at localities in the southern part of Rio Blanco County. This locality is west of the continental divide and far north.

[14] The following botanical papers discuss quite fully the ecology of the eastern lower foothills and mesas of northern Colorado: RAMALEY, FRANCIS, Botany of northeastern Larimer County, Colorado. Univ. Colo. Studies **5**:119–131. 1908. RAMALEY, FRANCIS, AND ROBBINS, W. W., Ecological notes from north-central Colorado. *Ibid.* **5**:111–117. 1908. ROBBINS, W. W., Studies of mesa and foothill vegetation; 4. Deciduous trees and shrubs of the mesas. *Ibid.* **6**:36–49. 1908. ROBBINS, W. W., AND DODDS, G. S., Studies in mesa and foothill vegetation; 3. Distribution of conifers on the mesas. *Ibid.* **6**:31–36. 1908.

sion, the mesas are not subject to as late spring frosts as are the adjacent plains. Average length of growing season (period without frost) about 4 months, 21 days. *Relative humidity:* mean annual 48–50 per cent.

The lower foothills and mesas of northeastern Colorado represent the meeting ground of grass and forest formations. The trees here are Rocky Mountain yellow pine and Douglas fir (*Pseudotsuga mucronata* [Raf.] Sudw.), the latter occurring in the moister situations. The Rocky Mountain yellow pine meets the grassland formation on the lower parts of the mesas; this formation consists chiefly of *Bouteloua oligostachya* and *Koeleria cristata* (L.) Pers. *Cercocarpus parvifolius* Nutt., the mountain mahogany, and *Yucca glauca* are common on ridges. Other common shrubs of this region are *Prunus melanocarpa* (A. Nels.) Rydb., *P. pennsylvanica* L.f., *Symphoricarpos occidentalis* Hook., *Rhus trilobata* Nutt., *R. glabra* L., *Ribes longiflorum* Nutt., *R. pumilum* Nutt., *R. vallicola* Greene, *Opulaster* spp., *Ceanothus Fendleri* A. Gray, *C. pubescens* (T. and G.) Rydb., *Crataegus* spp., *Rosa Sayi* Schwein., *Berberis repens* Lindl., and *Edwinia americana* (T. and G.) Heller.

The lower foothills and mesas of southeastern Colorado differ from the corresponding regions in northern Colorado. The mesas are grassland composed chiefly of *Bouteloua oligostachya*. Scrub oak and mountain mahogany form a chaparral between the grassland and Rocky Mountain yellow pine formations of the lower foothills. Pinyon pine (*Pinus edulis* Engelm.), the one-seeded juniper (*Sabina monosperma* [Engelm.] Rydb.), and the Rocky Mountain juniper (*Sabina scopulorum* [Sarg.] Rydb.) are common in the lower portion of the foothills. The Rocky Mountain yellow pine and other foothill forms extend far out on the Arkansas-Platte Divide.[15]

EASTERN UPPER FOOTHILLS

Precipitation: mean annual 15–20 inches; about 75 per cent. during the growing season; the early summer is the season of maximum rainfall. *Temperature:* mean annual 40°–45°; mean summer 60°–65°; mean annual range

[15] For an extended account of the mesas and foothills of southern Colorado see the following papers: SHANTZ, H. L., A study of the vegetation of the mesa region east of Pike's Peak; the Bouteloua formation. BOT. GAZETTE **42**:16–47, 179–207. 1906. SCHNEIDER, E. C., The distribution of woody plants in the Pike's Peak region. Colorado Coll. Publ. Science Series **12**:137–170. 1909.

30°–40°; diurnal range decreases with an increase of altitude. Average date of last spring frost May 30 to June 31; average length of growing season 3 months, 21 days, to 3 months, 6 days. *Relative humidity:* annual amount greater than on plains and mesas.

This area extends the full length of the state along the eastern slope. It is between the altitudes of 6000 and 8000 feet. It is dominated by a forest of Rocky Mountain yellow pine and Douglas fir. The upper limit of the zone is coextensive with the upper limit of abundant growth of Rocky Mountain yellow pine. South Park, although mostly above 8000 feet, has a foothill vegetation and should be classed as upper foothill country. It is much drier than localities at the same altitudes on the eastern slope. It is an upland country supporting a xerophytic vegetation.[16]

MONTANE ZONE

Precipitation: mean annual 15–20 inches; many localities have greater amounts; July and August are the wettest months; snow abundant. *Temperature:* mean annual 35°–40°; mean summer 55°–60°; mean annual and diurnal ranges of temperature generally small but varying greatly with exposure. No data for average date of last spring frost and average length of growing season. *Relative humidity:* fluctuating between high and low; annual amount increases with increase of altitude.

This zone roughly includes those portions of the state with an altitude between 8000 feet and 10,000 feet. On the western slope and on the minor mountain ranges and plateaus of the western part of the state, the montane zone often extends to higher altitudes, which is due chiefly to the generally drier condition of this slope.

The vegetational composition and appearance of the montane zone varies in different sections of Colorado. In the northeastern part of the state it is dominated by lodgepole pine, being adjoined by the Rocky Mountain yellow pine forests of the foothills and the Engelmann spruce forests of the subalpine regions. Other less abundant conifers of this zone are the bristle cone pine (*Pinus aristata* Engelm.), limber pine (*Pinus flexilis* James), Colorado blue spruce (*Picea Parryana* [Andree] Sarg.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). In southern Colorado lodgepole pine does

[16] RAMALEY, FRANCIS, Plants of the Florissant region in Colorado. Univ. Colo Studies **3**:178–185. 1906.

not form so extensive forests as it does in the northern part of the state. East and west of the continental divide the white fir (*Abies concolor* Lindl.) occurs in the montane zone of southern Colorado, but not in the northern part. Aspen (*Populus tremuloides* Michx.) is common throughout the montane zone in all parts of the state, but particularly so on the western slope. There it covers extensive areas and grows to a considerable size. In northwestern Colorado it often dominates extensive areas, or may be mixed with lodgepole pine. Here oak shrubbery is often abundant in the lower parts of the zone. In southwestern Colorado the montane zone extends between the altitudes 9000 feet and 10,500 feet and is chiefly aspen-covered.

SUBALPINE ZONE

Precipitation: mean annual above 20 inches; often 35 or 40 in some localities; maximum amount in the summer; daily afternoon showers common. *Temperature:* mean annual below 35°; mean summer below 55°; mean annual and diurnal ranges low. *Relative humidity:* fluctuating between high and low but generally high.

In all parts of the state, except the extreme southern part, this zone extends from an average altitude of 10,000 feet to timber line; it is the highest timbered zone. The dominant and characteristic tree in all parts of the state is the Englemann spruce. It is nearly always accompanied by limber pine and subalpine fir. Other common trees and shrubs are *Salix chlorophylla* Anders., *S. glaucops* Anders., *S. Bebbiana* Sarg., *S. pseudolapponum* Seem., *Betula glandulosa* Michx., *Ribes parvulum* (A. Gray) Rydb., *R. lentum* (Jones) Coville & Rose, *Sambucus microbotrys* Rydb., and *Lonicera involucrata* Banks. *Vaccinium oreophilum* Rydb. and *V. caespitosum* Michx. are common shrubs growing on the forest floor. Meadows and swampy areas are abundant throughout the zone.

TIMBER LINE.—Timber line is the upper limit of tree growth. In Colorado it usually marks the limit above which trees are climatically excluded. HARVEY[17] has pointed out that timber line on Mt. Ktaadn in Maine is not climatic but physical. COOPER,[18] although

[17] HARVEY, L. H., A study of the physiographic ecology of Mt. Ktaadn, Maine. Univ. Maine Studies. 1903.

[18] COOPER, W. S., Alpine vegetation in the vicinity of Long's Peak, Colorado. BOT. GAZETTE **45**:319–337. 1908.

recognizing timber line to be a climatic division line, has shown that in the Long's Peak region, Engelmann spruce has not reached the point where tree growth is climatically excluded, and that the present timber line as represented by Engelmann spruce is not the true climatic timber line. In this region, however, limber pine forms a true climatic timber line.

The average height of timber line in Colorado is near 11,500 feet. It is higher on the ridges than in the gulches, on south and west exposures than on north and east exposures. Engelmann spruce, subalpine fir, and limber pine are the principal timber line trees.

ALPINE ZONE

Climatic conditions for this zone in Colorado are not well known. The lower limit of the alpine zone is timber line. Although precipitation is ample and the relative humidity frequently high, tree growth is absent partly because of the thin soil, steep slope which cannot retain sufficient moisture, low air and soil temperatures, high winds, snow,[19] rapid transpiration, and liability to frosts. The lower portions of the zone are covered with grasses and low alpine mat forms. The upper parts are usually rock fields supporting little except a lichen vegetation.

Some of the most common alpine plants of Colorado are *Deschampsia caespitosa* (L.) Beauv., *Phleum alpinum* L., *Trisetum subspicatum* (L.) Beauv., *Festuca brachyphylla* Schultes, *Carex atrata* L., *Polygonum viviparum* L., *Silene acaulis* L., *Caltha leptosepala* Hook., *Dryas octopetala* L., *Clementsia rhodantha* (A. Gray) Rose, *Sieversia turbinata* (Rydb.) Greene, *Castilleja occidentalis* Torr., *Campanula petiolata* DC, *Mertensia alpina* (Torr.) Don., *Rydbergia grandiflora* (T. and G.) Greene, *Artemisia scopulorum* A. Gray, *Eritrichium argenteum* Wight, *Trifolium dasyphyllum* Torr., *T. Parryi* A. Gray, and *Tetraneuris lanata* (Nutt.) Greene.[20]

[19] SHAW, C. H., Causes of timber line on mountains. Plant World 12:169–181. 1909.

[20] For a list of the alpine plants of Colorado with statistics of their geographical distribution, see article by COCKERELL, T. D. A., Alpine flora of Colorado. Amer. Nat. 40:861–873. 1906.

SAN LUIS VALLEY

Precipitation: mean annual below 10 inches; about 75 per cent. during growing season; July and August wettest months; small amount of snow. *Temperature:* mean annual 40°–45°; mean summer 60°–65°; mean annual and daily range great. Average date of last spring frost May 24 to June 12; average length of growing season (period without frost) 3 months, 15 days. *Relative humidity:* low.

This dry, level country is covered with *Artemisia tridentata*, which spreads over extensive areas, the plants often reaching a height of 8 feet. *Chrysothamnus* spp., *Sarcobatus vermiculatus*, and *Atriplex* spp. are abundant, alternating in some places with bunch grasses. On the slopes occur pinyon pines, cedars, and Rocky Mountain yellow pines. The higher plant zones are very similar to corresponding zones in other parts of southern Colorado.

The level parts of San Luis Valley have the same altitude as the eastern foothill region (7000–9000 feet). The climatic conditions are practically the same, with the exception of the precipitation and the daily and annual ranges of temperature. In the eastern foothills the precipitation is 15–20 inches; in San Luis Valley below 10 inches. In the eastern foothills the ranges of temperature are considerably less than in San Luis Valley. In comparing the monthly temperatures of Garnett, San Luis, and Saguache, all in San Luis Valley, with Idaho Springs, Georgetown, and Silver Cliff, all within the eastern foothills, it was found that, although the mean summer and mean annual temperatures were about the same, the winters of San Luis Valley are much severer than those of the foothills, the months of December, January, and February being 10°–15° colder. As a result of these differences in range of temperature and rainfall, the foothills support a forest growth, while grass and sage predominate in San Luis Valley.

MIDDLE PARK

Climatological data for this region are not sufficient to be of much use. It is very probable, however, that the lower and flatter portions of the park have nearly 10 inches of rainfall. There are great extremes of temperature. *Artemisia tridentata* produces the principal formation on the dry, level stretches. It is associated with *Chrysothamnus*

spp. and *Symphoricarpos oreophilus* A. Gray. Other common shrubs growing on dry hillsides are *Kunzia tridentata* (Pursh) Spreng., *Amelanchier elliptica* A. Nels., and *Holodiscus dumosus* (Nutt.) Heller. Grassland alternates with the sage in mesophytic level places. The hills, except south exposures, are covered with lodgepole pine. Engelmann spruce occurs in the deep and narrow canyons, even in the lower parts of the park, but it is not abundant below 9000 feet. Rocky Mountain yellow pine is very uncommon in Middle Park.[21]

WESTERN SAGE PLAINS AND LOWER FOOTHILLS

Under this head will be discussed that portion of the state west of the continental divide, which extends up to the montane zone, with the exception of Middle Park.

Precipitation: below 10 inches in the western part and 10–15 inches in the eastern part; about 50 per cent. during the growing season. *Temperature:* mean annual 40°–50° and above; mean summer 60°–70° and above; mean annual range above 45; diurnal range great. *Relative humidity*: generally low.

The dominant forms of vegetation of this area are sage brush, pinyon pine, scrub oak, and Rocky Mountain yellow pine. The northwestern part of the state, however, has climatic conditions which are appreciably different from those of the middle and southwestern part (see *figs. 5* and *6*). In the former area the mean annual and mean summer temperatures are about 5° cooler than in the southwestern area, and although the precipitation is about the same in amount and distribution, the effect of the lower temperature is indicated by the lower altitudinal distribution of typical arborescent forms. In northwestern Colorado, Rocky Mountain yellow pine grows to some extent on slopes between 6000 feet and 8000 feet; scrub oak occurs between the same altitudes; aspen comes in abundantly at 7500 feet, and scattered groves are found at lower elevations. In southwestern Colorado, Rocky Mountain yellow pine is not abundant below 8000 feet; scrub oak is seldom abundant below 8000 feet, and aspens do not occur commonly below 9000 feet.

In southwestern Colorado along streams, *Populus angustifolia*, *Lonicera involucrata*, and *Lepargyraea argentea* (Nutt.) Greene are

[21] The writer is not sufficiently familiar with conditions in North Park to discuss them.

common. Sage plains stretch from the streams to the foothills; associated with the sage is *Sarcobatus vermiculatus*. Other characteristic shrubs are *Fendlera rupicola* Engelm. & Gray, *Peraphyllum ramosissimum* Nutt., *Kunzia tridentata*, *Cercocarpus parvifolius*, *Amelanchier alnifolia* Nutt., and *Yucca baccata* Torr. The alkaline flats are covered with chenopodiaceous plants.[22] The foothills up to 7500 feet are covered with pinyon pines and cedars. Above these come Rocky Mountain yellow pine, forming a distinct zone up to 9000 feet.

As in southwestern Colorado, the greater portion of middle and northwestern Colorado, up to an altitude of 7500 feet, is covered with sage brush, *Chrysothamnus* spp., and *Sarcobatus vermiculatus*. There is very little grassland country until an altitude of 7000 feet is reached. Oak chaparral grows to some extent below 7500 feet, but in many localities forms a distinct zone between the pinyon-cedar and montane zones. Pinyon pine and cedars are common associates here as in other parts of Colorado. On the lower slopes cedar is predominant, forming nearly 90 per cent. of the tree growth; at higher altitudes pinyon becomes relatively more abundant. Sage brush reaches the height of its development, both in size and numbers, on level expanses below 7500 feet; it extends up to 10,000 feet, however, being confined to dry ridges. *Populus angustifolia*, *Alnus tenuifolia* Nutt., *Lepargyraea argentea*, and *Crataegus* spp. are common streamside plants up to an altitude of 7000 feet. *Cercocarpus parvifolius*, *Amelanchier oreophila* A. Nels., *Symphoricarpos* spp., and *Kunzia tridentata* occur on dry and stony hillsides.

It is generally held that the vegetation and flora of the eastern slope is very different from that of the western slope. This is especially true for altitudes below 8000 feet. The vegetation of the alpine, subalpine, and to a less extent of the montane zones, however, is very similar on both slopes. Below 8000 feet the climatic and zonal

[22] For excellent discussions of the flora and vegetation of the southwestern part of Colorado see the following articles: BRANDEGEE, T. S., The flora of southwestern Colorado. Bull. U. S. Geol. and Geog. Surv. of the Territories (Hayden Survey) **11**: 227–248. EASTWOOD, ALICE, Report on a collection of plants from San Juan County in southeastern Utah. Proc. Cal. Acad. Sci. **6**:270–329. 1896. BAKER, CARL F., AND EARLE, F. S., Narrative accounts of collecting trips in southern and western Colorado in *Plantae Bakerianae*.

relations are quite different on the two slopes. On the eastern slope the foothill zone extends from an altitude of 8000 feet down to 6000 feet, and is an area timbered with Rocky Mountain yellow pine. On the western slope, localities between 6000 feet and 7500 feet are dry, having a precipitation 5 to 10 inches less than similar altitudes of the eastern slope; the vegetation is chiefly sage brush, associated with *Sarcobatus vermiculatus* and *Chrysothamnus* spp. Pinyon pine and cedars occur on the ridges. Rocky Mountain yellow pine is scattered in northwestern Colorado; it extends up to 8000 feet, but forms no distinct zone. Below 6000 feet east of the continental divide are grass-covered plains with a precipitation of 10–20 inches. At the same altitudes on the western slope one meets with semi-desert conditions. The annual precipitation is below 10 inches and the vegetation is predominantly sage brush.

In general it may be said that the state west of the continental divide is drier from the vegetation standpoint than the eastern slope. Only about 50 per cent. of the rainfall on the western slope occurs during the growing season, in contrast with the occurrence on the eastern slope of about 75 per cent. during the same period. Hence for any two localities east and west of the continental divide with equal annual precipitation amounts, the locality west will have the more xerophytic vegetation.

In connection with the preparation of this paper, the writer wishes to express his deep appreciation of helpful suggestions and criticisms given by Professor FRANCIS RAMALEY.

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THE FLORAL DEVELOPMENT AND EMBRYOGENY OF ERIOCAULON SEPTANGULARE

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(WITH PLATES XIX AND XX)

Flowers

The inflorescence of *Eriocaulon septangulare* is a compact head of staminate and pistillate flowers. The two kinds of flowers are sometimes intermingled, but the most common arrangement is in groups of 10–30, all the members of each group exhibiting nearly the same stage of development. During the season there are usually about three successive groups of each kind of flower.

Longitudinal sections of the flower show that the parts appear in acropetal succession. The two sepals, and likewise the two petals, arise from the floral axis at somewhat different levels. This is probably to be interpreted, not as the survival of a primitive spiral arrangement, but as a result of the intercalary growth which is a marked feature especially of the inner flowers (*fig. 5*). Rudimentary carpels surrounding the tips of the floral axis occupy the center of the staminate flower (*fig. 1*), but do not progress beyond the stage shown in the figure; they can still be recognized readily in the old flowers. In the pistillate flowers the stamens are represented by rudimentary outgrowths put out above the petals and having their extremities of withered and blackened cells (*fig. 2*). Each flower is subtended by a bract and bears large conspicuous nectaries upon the petals. Transverse sections are shown in *figs. 3* and *4*. *Fig. 3b* and corresponding sections of the pistillate flowers show that the stamens belong to one cycle, and hence the flowers are tetracyclic.

The manuals describe this and other species of Eriocaulon as having the parts of the flowers in twos and threes, but in and about Lake Joseph, Ontario, where this material was collected, I have been able to find only the former type of flowers. Do these constitute a local race, or will other localities furnish similar examples of the constancy of dimerous symmetry?

Stamens

The stamens bear four narrow sporangia, whose hypodermal cell walls show the usual thickening, but not prominently so, and whose cavities before dehiscence unite in pairs. The pollen mother cells of each sporangium are in a single row, surrounded completely by a tapetum, and externally by two or sometimes three cell layers (*fig. 6*). They are somewhat flattened lengthwise of the anther, and in conformity with this peculiarity of shape and arrangement they exhibit an interesting polarity, the spindles of both divisions standing at right angles to the long axis of the sporangium. Many of the stamens fail to mature their microspores. The ripe microspores contain a large vegetative nucleus and two male cells. In good sections the latter can be seen to have an elongated pointed outline, and to be distinctly delimited from the remaining cytoplasm by a plasma membrane (*fig. 7*). The exine possesses strong thickening bands studded with minute spines (*fig. 8*).

Ovule and embryo sac

The position of the ovules and their relation to the carpels are illustrated in *fig. 5*. It will be seen that they are distinctly axial. They point outward at first toward the carpels, but gradually bend downward so that finally the micropyle is directed toward the base of the flower. The archesporial cell remains undivided for a long time, lengthening with the enlarging ovule (*figs. 9, 10*). Finally, without cutting off any parietal cell it segments into four megaspores, the innermost of which becomes the embryo sac (*fig. 10*). In a large number of cases several or all of the megaspores germinate, both by increase of size and by division of their nuclei. While thus increasing in size, some of them accommodate themselves to the space in which they lie by slipping past one another so as to lie side by side. Many cases somewhat similar to *fig. 12* were observed; also in sections of the same age as *fig. 13* a group of five or six nuclei above the embryo sac, and no doubt consisting of the unabsorbed nuclei of the sterile megaspores, can frequently be seen. But while it is perhaps the rule for more than one megaspore to germinate, I have never found two fully formed embryo sacs in one ovule, nor other than the lowermost megaspore the successful competitor.

About this time or a little later the nucellar tissue lateral to the megaspores begins to be broken down and absorbed by the growing embryo sac. A few of the apical cells of the nucellus, however, persist for a long time, and enlarging assume the appearance of a "tapetum" (*figs. 12–14, n*). These too are ultimately absorbed, and then the embryo sac abuts directly upon the inner integument and micropyle.

The development of the embryo sac is quite normal, so that little explanation need be added to the figures. The central vacuole first appears at the four-nucleate stage. During the three successive divisions there is little if any increase of nuclear material; probably the eight nuclei of *fig. 16* have no greater aggregate volume than the single nucleus of the megaspore.

In the succeeding pre-fertilization organization of the embryo sac some of these nuclei become greatly enlarged (cf. *figs. 16* and *18*, which are drawn to the same magnification). A nearly mature embryo sac is shown in *fig. 17*. The antipodals are never conspicuous. After the inception of endosperm formation they become difficult of recognition, but occasionally may be seen in a small pocket below the endosperm. The upper polar nucleus moves down to meet the lower one near the antipodals. From the frequency with which they are found in contact with each other, it may be inferred that their fusion is very gradual. It is attended with considerable growth of the fusing nuclei, and there is still further growth subsequent to their fusion (cf. *figs. 17, 18, 22*). Probably this enlargement of the definitive nucleus is correlated with the rapid production of endosperm consequent on fertilization. There is much variation among plants as to the time when the polar nuclei fuse and the relation of this fusion to pollination and fertilization. Thus in Elodea WYLIE (**15**) found that the actual presence of the pollen tube in the embryo sac is necessary to bring about the fusion. In Eichhornia (SMITH **14**) the fusion occurs before pollination, and in Sagittaria (SCHAFFNER **13**) before the entrance of the pollen tube. Further examples are given in COULTER and CHAMBERLAIN'S *Morphology of angiosperms* (**6**, pp. 95, 96). There can be no doubt that in Eriocaulon the fusion is independent of the stimulus of pollination, for it was found complete in numerous heads taken from beneath the surface of the water. On

the other hand, division of the endosperm nucleus does not appear to take place in the absence of fertilization.

Beneath the embryo sac there is a group of strongly thickened cells which probably function as conduction tissue. They stain deeply, and occasionally one of them proliferates into the embryo sac (*fig. 19*).

Fertilization

Fertilization was not observed in a sufficient number of cases to make possible a very definite description of the process. The observations indicate that the pollen tube entering the micropyle passes through one of the synergids or between them without destroying either. The contents of the undischarged tube shown in *fig. 20* could not be made out, but there can be no doubt that both of the male cells or their nuclei enter the embryo sac. Three or four cases similar to *fig. 22* were seen, and once I found a sperm nucleus (which had then lost its cytoplasmic sheath) about half-way between the egg and the definitive nucleus. Pollination and fertilization are apparently effected in the first flowers within the first day of their emergence from the water. The sexual nuclei in the egg fuse without delay, and their fusion is soon followed by that of the second sperm and the definitive nucleus.

Only one case of polyembryony was observed, the three embryos apparently originating from the two synergids and the egg (*fig. 34*).

Endosperm

The first division of the endosperm nucleus was not seen. The nuclei multiply rapidly, so that 16–32 of them are distributed about the periphery of the embryo sac before the first segmentation of the egg. They are elongated and flattened, and invariably take a position in the inner border of the parietal cytoplasm (*fig. 23*). When their number is about 64, tissue formation begins by the appearance of delicate walls across the cytoplasmic layer. The walls appear first in the micropylar and antipodal regions, and somewhat later about the sides of the embryo sac. At this time the inner boundary of the cytoplasmic layer has no definite wall (*fig. 24*), and the general appearance is similar to that figured and described by LAWSON (11) as occurring in the gametophyte of Cryptomeria;

but the analogy stops here. In Eriocaulon the endosperm cells are never binucleate and the first-formed walls are permanent.

The cells continue to extend centripetally by vacuolization, and then undergo periclinal division, resulting in an outer layer of flat cells which do not divide further, and an inner layer of larger cells (*fig. 25*). At this time no starch is present. The inner layer by further divisions obliterates the central cavity of the embryo sac and then rapidly fills with starch grains. In the ripe seed three regions of the endosperm are recognizable: (1) the outer layer, still more flattened and containing little starch; (2) the large thin-walled cells of the interior, with abundant starch; (3) a deeply staining group of starch-containing and elongated cells near the base.

Embryo

It is in the development of the embryo that this plant deviates more widely from ordinary angiosperms. The first division is, as usual, transverse (*fig. 27*). Each of the two resulting cells then divides in a longitudinal direction, the one toward the base of the sac dividing first as a rule (*figs. 28, 29*). The next divisions are also longitudinal, and at right angles to the preceding (*fig. 30*). Thus the embryo has no suspensor whatever, and passes through regular quadrant and octant stages. While these divisions are taking place, the embryo becomes globular in form and its cytoplasm beautifully vacuolated. The octant division is followed by the cutting off of a dermatogen. The process is not simultaneous in the two halves. Thus in *figs. 31* and *32* it will be seen that the micropylar half has divided most rapidly, while in *fig. 35* it is the basal half. The embryo of the ripe seed is shown in *fig. 36*. It is bell-shaped with flaring edges, and quite frequently the edges are upturned, owing to the pressure of the endosperm. There is no differentiation of the embryonic organs, nor any indication where these shall have their origin.

It is doubtful if a comparison of the early segmentation of the embryo is of value in determining relationship. There is too much variation within certain orders, and often the peculiarities are too manifestly adaptive. The nature of the endosperm and the embryonic organs is much more significant.

I have found no detailed study of plants nearly related to Erio-

caulon. In other plants mature undifferentiated embryos have been reported within recent years in numerous instances; for example, in Aigenetia (KUSANO **10**) and Peperomia (CAMPBELL **2**); also Gunnera (MODILEWSKI **12**) has no suspensor, and Piper (JOHNSON **8**) but a slight one. But undoubtedly the nearest parallels to the embryo sac of Eriocaulon as yet described are among the Araceae and the Nymphaeaceae. Thus in Arisaema (GOW **7**) the mature embryo sac is globular and without differentiation of organs; but its first three cells are in a row, and its early divisions are less regular. From CAMPBELL'S studies of the Araceae (**1, 3, 4**) it appears that the globular form of the embryo is characteristic of that order. But the embryos figured by him show far more irregularity in their development than is the case in Eriocaulon. CAMPBELL regards the absence or slight development of the suspensor (as in Aglaonema **1** and Spathicarpa **3**) as correlated with the complete investment of the embryo by endosperm tissue. In all the Araceae examined the endosperm was found to be septate from the beginning. The same is the case in Gunnera. It will be seen, however, that this explanation will not apply to the lack of a suspensor in Eriocaulon, since divisions of the embryo up to the octant stage precede tissue formation in the endosperm, and even for some time afterward the walls of the endosperm are too weak to exert much pressure. Pistia, another aroid, was investigated by HEGELMAIER (**8**) in 1874, and its embryo as described by him is in its early history practically identical with that of Eriocaulon. It shows the same regularity of form and sequence up to the cutting off of the "dermatogen-like outer layer," and for some time thereafter, except that for a time in individual cells of this layer periclinal divisions now and then occur, a phenomenon I have not observed in Eriocaulon. In the ripening seed of Pistia the globular embryo becomes indented, and root tip and cotyledon are developed.

Somewhat similar embryos occur in *Castalia odorata* and *Nymphaea advena* (COOK **5**) and in Nelumbo (YORK **16**). These are described as passing through quadrant and octant stages, less regular than those of Eriocaulon and Pistia. The case of Nymphaea is particularly interesting. Though the extent of the dermatogen is not stated, from the figures it appears to invest the embryo completely,

and there is no trace of a suspensor. Later, however, after the position of the cotyledon is indicated, a short suspensor is developed through the activity of one of the basal cells.

Experiments are now in progress to ascertain what changes the embryo of Eriocaulon undergoes in germination.

Summary

1. Eriocaulon gives evidence of derivation from a bisporangiate ancestor in that the pistillate and staminate flowers possess rudimentary stamens and pistil respectively.

2. The flower is tetracyclic.

3. The ovules are placed laterally upon the axis.

4. Four megaspores are produced, the innermost of which is fertile, but the others in a large number of ovules begin germination.

5. The embryo sac develops in the usual way.

6. "Double fertilization" occurs.

7. The embryo has no suspensor; its first division wall is transverse; quadrant, octant, and periclinal divisions follow; and no embryonic organs are recognizable in the ripe seed.

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EXPLANATION OF PLATES XIX AND XX

All the figures were drawn with the aid of an Abbé camera and a Leitz microscope, and have been reduced one-half in reproduction. The reference letters are as follows: *b*, bract; *s*, sepal; *p*, petal; *a*, stamen; *c*, carpel; *t*, tapetum; *n*, apex of nucellus.

FIG. 1.—Longitudinal section of staminate flower. ×105.

FIG. 2.—Longitudinal section of pistillate flower. ×105.

FIG. 3*a*.—Transverse section of staminate flower. ×105.

FIG. 3*b*.—Transverse section of same flower at the level of the origin of the stamens; *p*, petals and gland. ×105.

FIG. 4.—Transverse section of pistillate flower. ×105.

FIG. 5.—Superficial view of pistillate flower with bract (*b*), sepals (*s*), and petals (*p*) removed; ovules and apex of flower axis seen through the ovary wall. ×80.

FIG. 6*a*.—Transverse section of a microsporangium at the mother cell stage. ×730.

FIG. 6*b*.—Part of longitudinal section of microsporangium of same age as the preceding. ×730.

FIG. 7.—Section of mature microspore. ×730.

FIG. 8.—Surface view of mature microspore. ×730.

FIG. 9.—Longitudinal section of ovary with archesporium. ×730.

FIG. 10.—Same at older stage. ×730.

FIG. 11.—The four megaspores. ×730.

FIG. 12.—Germination of megaspores. ×730.

FIGS. 13–17.—Successive stages in development of embryo sac. ×730.

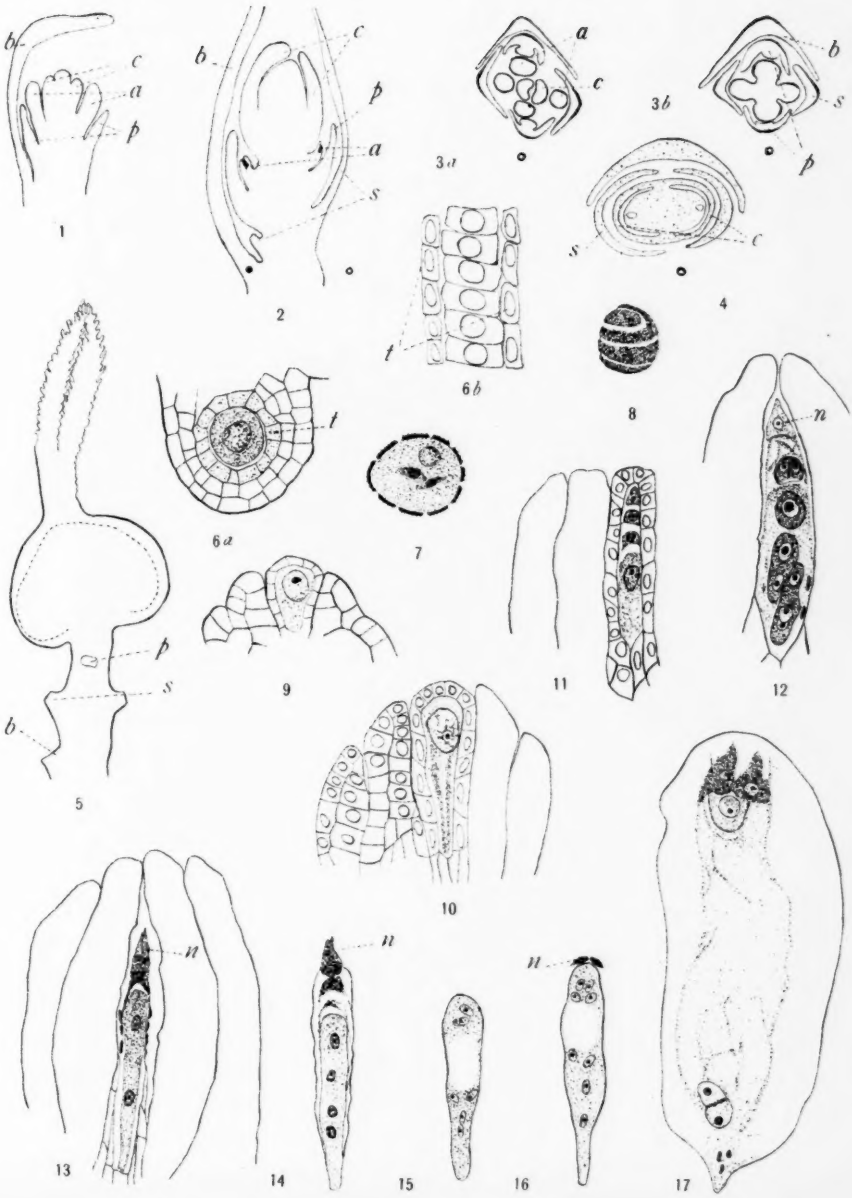
FIG. 18.—Definitive nucleus before fertilization. ×730.

FIG. 19.—Proliferation into the base of the embryo sac. ×730.

FIG. 20.—Egg apparatus and entrance of pollen tube. ×730.

FIG. 21.—Egg apparatus after fertilization. ×730.

FIG. 22.—Fusion of second male nucleus with definitive nucleus. ×730.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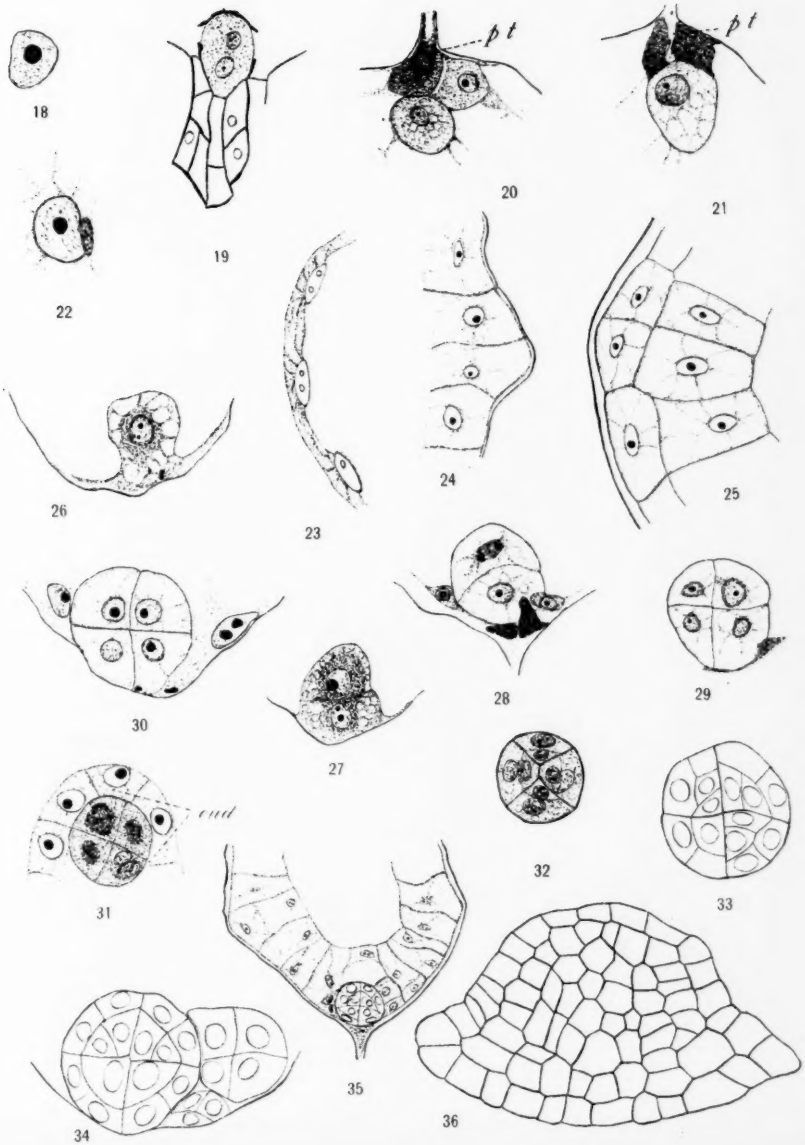
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FIG. 23.—Endosperm before tissue formation. ×730.

FIG. 24.—Tissue formation in endosperm. ×490.

FIG. 25.—Division of parietal layer of endosperm. ×730.

FIG. 26.—One-celled embryo. ×730.

FIG. 27.—Two-celled embryo. ×730.

FIG. 28.—Second division of embryo. ×730.

FIG. 29.—Quadrant stage of embryo. ×730.

FIG. 30.—Octant stage of embryo. ×730.

FIG. 31.—Transverse section of inner half of embryo, showing origin of dermatogen. ×730.

FIG. 32.—Transverse section of micropylar half of same embryo. ×730.

FIG. 33.—Transverse section of an older embryo. ×730.

FIG. 34.—Polyembryony.

FIG. 35.—Micropylar end of embryo sac, showing embryo and endosperm. ×240.

FIG. 36. Longitudinal section of embryo of mature seed. ×730.

THE CLOSING RESPONSE IN DIONAEA[1]

WILLIAM H. BROWN AND LESTER W. SHARP

(WITH ONE FIGURE)

Despite the attention attracted during the past century by the extraordinary reactions of *Dionaea muscipula* Ellis, there remains much uncertainty with regard to many points in its behavior. This uncertainty has led the present writers to carry out the work here reported.

The structure of the leaf is so well known that its description here is unnecessary. It may be well, however, to recall the fact that the leaf blade consists of two valves, each of which bears upon its upper surface three short, rather stiff bristles. Mechanical contact with these bristles causes the two valves to close together upon each other.

Relation of intensity to number of stimuli

DARWIN (3), SACHS (9), BATALIN (1), DETMER (4), MUNK (7), and others held that one contact stimulus was sufficient to produce the closing response. DARWIN (3) and BURDON-SANDERSON (2) showed that an extremely slight stimulus might be inadequate, while MACFARLANE (6) concluded from his researches that under ordinary conditions two mechanical stimuli are always necessary. In investigating this question it is of course necessary to avoid all possibility of shaking, which might cause uncertainty as to the number of stimuli applied. In the present experiments a stiff straw was so supported that it could be adjusted to any desired position and moved mechanically by means of a rack and pinion and milled head. By this method the movement of the straw could be accurately controlled, and the number of stimuli definitely known.

Leaves of plants which had been kept at 15° C. for one to two hours were stimulated by pressure upon one of the sensitive hairs, and it was found that closure almost never resulted after one such stimulus, even though the hair was bent down so as to touch the

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 12.

leaf. If, however, a second stimulus was applied either on the same or another hair, after an interval of 1.5 to 20 seconds the leaf responded, and in nearly every case by complete closure. The leaves of plants which had been kept about the same length of time at 35° C. frequently responded to one contact stimulus, while those kept at 40° C. closed with the first stimulus about as often as with the second. Slight individual differences were sometimes found in the leaves tested. These results seem to show that while under ordinary conditions two mechanical stimuli are usually necessary for closure, the number is not fixed, but varies with the environment and to some extent with different leaves.

The question now arises as to whether a certain amount of stimulation, rather than a certain number of stimuli, is required to effect closure. This was first investigated by the use of electrical stimuli, the intensity of which could be accurately controlled. MACFARLANE (**6**) was inclined toward the belief that two electrical shocks are necessary to cause the closing response.

Two series of experiments were carried out, in one of which the terminals of an induction coil were connected by wires with the petiole and keel, and in the other with the petiole and a sensitive hair. These connections were made by one gentle touch in such a manner as not to cause closure as a result of contact. The leaves were allowed five minutes in which to recover from any after-effect of the contact stimulus. They were then stimulated with opening shocks at intervals of 15 seconds, a single dry cell being used in the primary circuit. The result in both series was essentially the same, the number of shocks necessary to cause closure increasing as the intensity of the stimulus decreased. One strong shock was always sufficient to cause the response, but when weaker shocks were applied the number increased until in one case 26 were required. As with mechanical stimuli, the leaves showed slight individual variations. These results are shown in table I, in which the numbers indicating the position of the sliding secondary coil indicate the intensity of the induced current produced, the greatest electromotive force corresponding, of course, to the position marked 0, while the lowest corresponds to position 6. The effect of a stronger current, obtained by the use of two cells in place of one in the primary circuit, was

tested at position 0, but no difference was observable between the response in this case and that in which only a single cell was used. Partial closures were obtained before the complete closures in four cases with the first arrangement of contacts, and in a single case with the second arrangement. These are indicated by footnotes below the table.

TABLE I

NUMBER OF ELECTRIC SHOCKS REQUIRED TO PRODUCE COMPLETE CLOSURE WITH VARYING INTENSITY OF CURRENT; SHOCKS AT INTERVALS OF 15 SECONDS

CONTACT ON SENSITIVE HAIR AND PETIOLE									CONTACTS ON KEEL AND PETIOLE							
Position of coil	No. of test	0	½	2	3	4	5	6	Position of coil	No. of test	0	½	2	3	4	5
Number of shocks required for complete closure	1	1	1	1	4*	6‡	7	10¶	Number of shocks required for complete closure	1	1	1	2	1	3†	4
	2		2	2	3‡	1†		26		2		1	2	2	2	5
	3		1							3		1				
Average		1.0	1.3	1.5	3.5	3.5	7.0	18.0	Average		1.0	1.0	2.0	1.5	2.5	4.5

* Partial closure with 3 shocks.
† Partial closure with 2 shocks.
‡ Partial closure with 5 shocks.
¶ Partial closure with 9 shocks.

It is apparent from these tests that closure is due to intensity of stimulation rather than to number of stimuli, and that there exists a definite after-effect with a duration of over 15 seconds, the summation of these after-effects finally producing the response in the case of the weaker electric shocks.

We have heretofore considered mechanical stimuli as though all were of the same intensity, a condition which appears to be true if the hair is markedly bent. As has been stated, leaves kept at a temperature of 15° C. usually close on the application of the second stimulus, and in this case it appears to make no difference whether the bending of the sensitive hair is comparatively slight, or great enough to bring the hair against the leaf. At higher temperatures the leaf responds to one stimulus as frequently with slight as with more marked bending of the sensitive hairs. This is shown even more conclusively by the fact that at a temperature of 15° C. the leaf fails to respond when the hair is bent down against the leaf by one movement, while less bending, if accomplished by two movements, brings about response.

If, however, the bending is so slight as to be scarcely apparent, three to five stimuli, rather than two, are usually necessary to produce response. It appears, in general, that in both mechanical and electrical stimulation closure is due to the amount of stimulation rather than to the number of stimuli, but the amount of stimulation appears not always to be proportional to the amount of bending of the sensitive hair. If this is true, the number of contact stimuli necessary to cause closure should increase with the length of the time

TABLE II

RESPONSE TO CONSECUTIVE CONTACT STIMULI AT VARYING TIME INTERVALS

TIME INTERVAL BETWEEN STIMULI	NO. OF EXPERIMENT	NUMBER OF STIMULI								
		1	2	3	4	5	6	7	8	9
20 seconds	1	−	+							
	2	−	+							
	3	−	+							
	4	−	+							
1 minute	1	−	P	+						
	2	−	P	+						
	3	−	−	P	+					
	4	−	−	−	P	+				
2 minutes	1	−	−	−	P	+				
	2	−	−	−	−	P	+			
	3	−	−	−	−	P	+			
	4	−	−	−	−	P	+			
	5	−	−	−	−	−	P	+		
	6	−	−	−	−	−	P	+		
3 minutes	1	−	−	−	−	−	P	P	+	
	2	−	−	−	−	−	−	P	P	+
	3	−	−	−	−	−	−	−	P	+

interval between them, since the effect of stimulation would be expected to disappear to a greater extent as the length of the time interval is increased. This hypothesis was tested with the result that leaves at a temperature of 15° C., stimulated mechanically at intervals of 20 seconds, closed with the second stimulus; when the interval was increased to a minute, they responded with 2 to 5 stimuli; at intervals of 2 minutes, a response was produced with 5 to 7 stimuli; while at intervals of 3 minutes, about 6 to 9 stimuli were necessary to bring about closure. These results are shown in table II, in which − denotes no response; P, partial closure; +, complete closure.

It is seen at once that with increasing length of time interval the number of stimuli required to produce a response increases also. Considering only the number of stimuli required for complete closure, these results are tabulated in table III.

TABLE III

NUMBER OF STIMULI NECESSARY TO PRODUCE COMPLETE CLOSURE, THE TIME INTERVAL VARYING FROM 20 SECONDS TO 3 MINUTES

EXPERIMENT NO.	TIME INTERVALS BETWEEN STIMULI			
	20 seconds	1 minute	2 minutes	3 minutes
1	2	3	5	8
2	2	3	6	9
3	2	4	6	9
4	2	5	6	
5			7	
6			7	
Average	2.0	3.8	6.2	8.7

The averages from this table are plotted on the graph of *fig. 1*, in which the abcissas represent the length of the time intervals between stimuli, and the ordinates the average number of stimuli required for complete closure. In this region the graph shows only a slight curvature. It is nearly a straight line, which would seem to denote that at intensities ranging from 20 seconds to 3 minutes—and of course for these particular plants—the number of stimuli necessary for complete response varies almost directly with the length of the intervals.

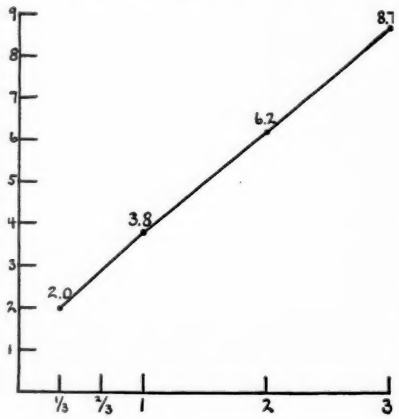

Fig. 1

It may be concluded from the foregoing that leaves seem to respond by closing to a definite amount of accumulated effect, possibly the

production of some chemical substance as the result of excitation; that the amount of this effect varies with the intensity of the stimulus; and that the amount of stimulation necessary for closure varies with different leaves, probably with different conditions of the plant.

Localization of perception

DARWIN (**3**) held that the surface of the blade is very slightly, and the footstalk not at all sensitive. MACFARLANE (**6**) showed that scraping the surface or squeezing the blade with steel forceps would cause closure, and concluded that "the leaf of Dionaea, then, is truly sensitive throughout its halves to mechanical stimulation, but the capacity for receiving sensation impulses is highly concentrated in the hairs." This writer states, however, that two pinches with the forceps are required to cause closure. In our experiments, leaves responded to one, two, or even more such pinches, according to the strength of the stimulus and the condition of the leaf. It thus appears that MACFARLANE'S conclusion is supported, in that all parts of the leaf are sensitive, and the question is raised whether the protoplasm of all parts may not be equally sensitive to stimulation, and that the hair functions simply as a mechanism which compresses certain cells. OUDEMANS (**8**) and BATALIN (**1**) came to the conclusion that the base of the hair is the sensitive region, while HABERLANDT (**5**) has pointed out near the base of the hair a layer of cells which appear especially fitted for being bent, and thus having their contents compressed. The latter author considered this layer the sensitive region, and expressed surprise that the rest of the leaf should be sensitive at all.

When a hair is stimulated by contact, it is first bent laterally and downward, held in this deformed position for a short time, and then allowed to spring back to its original position. If stimulation be due to a compression of cells at the base of the hair, the downward movement alone should cause closure. To test this, a stiff straw was supported as in former experiments, so that it could be accurately adjusted and held definitely in any position. Two downward thrusts on the same sensitive hair without an intervening release caused in every case at 15° complete closure. With a temperature

of 35° C. to 40° C. the leaves frequently responded to one downward thrust without a release.

When a sensitive hair was bent down and held mechanically in that position for 5 minutes, the leaf nearly always failed to respond. This experiment was repeated many times, but response followed in only a very few cases, and then only a few seconds after the contact. These exceptional closures seem to have been due to the downward thrust.

In order to determine the effect of the upward movement of the hair, the latter was bent down carefully against the leaf without causing closure, and held in that position for a period of 5 minutes in order that the effect of the compression stimulus might disappear. The hair was then allowed to spring back to its original position by two successive upward movements. This experiment was repeated many times, but the leaves never exhibited any response. The same operation was then repeated with the addition of alternate bendings and releases subsequent to the two upward movements, at intervals of 15 seconds. In no case did the leaf respond to a release, but always to a downward movement. The leaf is thus seen to respond only to a downward bending of the hair, and it seems probable that stimulation is due to a compression of the cells at its base, and that this compression is analogous to the compression of the cells of the blade when the latter is squeezed with forceps.

That the bending of the cells at the base is alone sufficient to cause response was shown in the following manner. A hair was cut off near the base and the leaf allowed ample time to recover from any possible shock produced by the cutting. The remaining portion was then pressed with a needle. In this operation it could be seen by means of a lens that bending took place only in the region where lie the cells shown by HABERLANDT to be especially suited to a compression stimulus. In such cases the leaves responded normally. That simple bending of the sensitive hair, without contact with a hard object, is sufficient to cause closure was shown by directing jets of air against it, when the leaf responded as if stimulated by contact.

We have seen that all parts of the leaf are sensitive to mechanical pressure, and that the hair probably functions as a mechanism for the compression of certain cells. It next remains to be seen whether

the protoplasm of these cells is more sensitive than that of the other cells of the leaf. Inspection of table I will show that when electrical shock was conducted through the keel to the petiole, and therefore not passed through the region at the base of the hair, it was just as effective, or perhaps slightly more so, than when passed through the sensitive hair itself.

It was found that water at room temperature when carefully applied to either surface of the leaf blade does not cause it to close. Water at 65° C., however, will cause closure without harming the leaf, and this response is just as marked, so far as could be determined, when the water is applied to the back of the leaf as when applied to the inner surface or to the bases of the sensitive hairs. These experiments with heat and electricity seem to indicate that the other cells of the blade are just as sensitive as those at the bases of the hairs. Contrary to DARWIN's opinion, the petiole is also sensitive, as we have found that passage of electrical shocks through it will cause closure of the valves. In this case, however, a much stronger stimulation is required to effect closure than when the shock is applied directly to the blade. This difference may very well be due to loss in conduction of the stimulus from the petiole to the region of bending.

Stimuli of various forms

In the experiments already recorded, it has been shown that closure may result from the application of mechanical, electrical, and thermal stimuli. DARWIN (**3**), MACFARLANE (**6**), and others have shown that the leaf may also be closed as the result of chemical stimulation. For convenience, these various kinds of stimuli may be discussed separately.

MECHANICAL STIMULI.—It has been seen that all parts of the leaf are sensitive to mechanical stimulation, and that this acts through compression of cells. DARWIN (**3**) states that water falling on the sensitive hairs does not cause closure, while MACFARLANE (**6**) observed that a steady stream directed against a hair, or the gradual immersion of the leaf, does cause the response. In our experiments it was found that the leaves could be filled carefully with water, or wholly immersed, without causing the response, but that the dropping of water on the hairs, or the movement of the leaf while immersed, caused it to close

if the hairs were thereby bent. The effect of water seems to be entirely due, therefore, to its mechanical action.

It is well known that a slight shaking will cause movement in the leaf of Mimosa. Experiments were undertaken to determine whether the leaf of Dionaea would also respond to shaking. These were not conclusive, but showed at least that the leaves can endure much shaking without showing response. In one case a long-petioled leaf was arranged so that it was struck near the distal end on alternate sides by the bar of a metronome beating 200 times per minute; and after 45 minutes the leaf showed no change. When the leaves of Mimosa are shaken, the large leaflets offer a considerable resistance to the air, which, together with their inertia, results in the bending of them and of the pulvini. The only parts of a Dionaea leaf which could be so affected are the cells at the bases of the sensitive hairs, as all the rest of the leaf is comparatively rigid. The hairs are so slender that they offer little resistance to the air, and on account of their small mass have a relatively slight inertia, and so when moved through the air can have little tendency to bend the cells at their bases. In experiments, however, in which the leaves were shaken under water, which offers a greater resistance to the passage of the hairs, the result was the same as in a Mimosa leaf shaken in air. It would thus seem that the nature of the response is the same in the two cases, the effect of the denser medium in the former balancing the effect of the large leaflets in the latter. This conclusion is further supported by the experiment already noted, in which the leaf closed as a result of bending produced in a sensitive hair by jets of air directed against it.

MACFARLANE (**6**) found that leaves stimulated twice mechanically at an interval of 0.25 second did not close on the second stimulus. If, however, the interval was 0.33 second or more they did close on the second stimulus.

Leaves which had been kept for an hour at 15° C. were stimulated twice mechanically at intervals of 0.25 to 2 seconds. When the interval was less than 0.75 second, response never followed; when it was 1 second, response was frequent; while at intervals of 1.5 seconds or more the leaves invariably closed. At temperatures of 35° C. to 40° C. the leaves rarely failed to respond to two mechanical stimuli separated by an interval of 0.25 second. They always

responded when the interval was longer than this and failed to respond with shorter intervals. This is added evidence that the leaves respond more readily at higher temperatures than at lower. As in the case of animal muscle, there seems to be in Dionaea a short interval after one stimulus during which another has no effect.

THERMAL STIMULI.—MACFARLANE (**6**) allowed drops of water at temperatures varying from 50° C. to 75° C. to fall upon open leaves. At the higher temperature one drop caused closure, while at the lower several applications were necessary. Only four of the leaves so treated reopened, and he says, "the subsequent fate of most of the leaves points to a permanent injury." It is not stated whether or not the water was dropped on the sensitive hairs. The present writers found that water at room temperature, dropped directly upon the hairs, causes closure, while the gentle application of water at 50° C. does not cause the response. When warm water is dropped in this manner, it is of course cooled somewhat before it reaches the leaf. Since it is possible to interpret the cases reported by MACFARLANE as being due either to a heat stimulus, to a mechanical stimulation of the sensitive hairs, or to injury, it was thought advisable to reinvestigate the effects of heat. Water at 65° C. was applied in some cases to the inner, and in other cases to the outer surface of the leaves. In all cases closure resulted. These leaves exhibited no appearance of injury, and after reopening responded again quite normally. As a control for these experiments, water at room temperature was applied for several minutes to both inner and outer surfaces of the leaves without effect. This seems to indicate that heat causes the closing response. Water at 75° C. was then applied as above. Closure resulted in all cases, but two days later the parts of the leaves touched by the water were dead and black. Only small areas on some of them had been injured, and in several such cases the rest of the leaf responded normally. We can also confirm MACFARLANE'S statement that cold water will cause closure. This is true whether it be applied to the inner or to the outer surface.

ELECTRICAL STIMULI.—Experiments already described show that electrical stimuli, when applied to various parts of the leaf and petiole, cause closure, and that the effect depends upon the intensity of the stimulation rather than upon the number of stimuli. The response

is brought about by either opening or closing shocks from an induction coil, but the former are much more effective than the latter. The feeble effect of closing shocks is shown by the fact that when as many as 100 of these were applied to leaves at intervals of 15 seconds, the coil being at position 0 (see table I), the leaves showed no sign of response. When the closing shocks were followed by opening shocks, the leaves responded to two of the latter as if nothing had preceded them. In another case two dry cells were used in the primary circuit, and the leaf closed on the 21st closing shock. Continuous current from a dry cell failed to cause closure.

EFFECT OF COMBINING STIMULI OF TWO FORMS.—As has been shown, leaves kept at 15° C. usually respond to two marked bendings of the sensitive hairs. A series of such plants was stimulated first by a single contact and then by an electric shock of such strength that two of these would be required to cause closure if used alone. These plants usually responded on the first electrical stimulus, while in two control series, in one of which only contact stimuli were used and in the other only electrical stimuli, they usually responded on the second stimulus. Table IV represents these three series.

TABLE IV

STIMULATION OF SENSITIVE HAIR BY MECHANICAL AND ELECTRICAL STIMULI

SERIES I HAIR STIMULATED BY ONE MECHANICAL CONTACT FOLLOWED BY OPENING SHOCKS				SERIES II HAIR STIMULATED ONLY BY OPENING SHOCKS OF THE SAME INTENSITY AS THOSE OF SERIES I		SERIES III HAIR STIMULATED ONLY BY MECHANICAL CONTACTS SIMILAR TO THOSE OF SERIES I	
Experiment number	Number of shocks required for complete closure			Experiment number	No. of shocks required for complete closure	Experiment number	No. of contacts required for complete closure
	Mechanical	Electrical	Total				
1.....	1	1	2	1	2	1	2
2.....	1	1	2	2	2	2	2
3.....	1	1	2	3	3	3	2
4.....	1	2	3	4	2	4	2
5.....	1	1	2	5	2	5	2

The results given in table IV seem to show that stimuli of different forms produce a similar internal effect, and that the leaves respond, as has already been pointed out, only with the accumulation of a certain amount of this effect.

Summary

The closing response in Dionaea depends upon the intensity rather than upon the number of stimuli, the number of stimuli required varying in the inverse order of their intensity.

Response is normally brought about by the compression of certain cells at the bases of the sensitive hairs, but the compression of other cells of the blade also causes closure, and it is probable that the latter cells are equally sensitive with the cells at the bases of the hairs, as is indicated by electrical and thermal stimulation.

The closing response follows the application of mechanical, electrical, and thermal stimulation. It also follows a combination of stimuli of two kinds when consecutively applied, the individual stimuli being of an intensity such that either alone would be insufficient.

The effect of mechanical stimulation is due to compression of cells, and not to contact with a hard object, continued pressure, or release of pressure. The failure of the leaf to respond to shaking is probably connected with the small inertia of the sensitive hairs, and the slight resistance offered by the air to their passage through it.

Water at room temperature causes closure only when it bends a sensitive hair.

After one mechanical stimulus there is a short period during which a second mechanical stimulus is ineffective.

The writers are indebted to Dr. W. D. HOYT for collecting the plants used, and for help during the course of the work; to Professor D. S. JOHNSON for his encouraging interest; and to Professor B. E. LIVINGSTON for valuable aid in the preparation of this paper.

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BRIEFER ARTICLES

AN ABNORMAL BRACT-MODIFICATION IN COTTON

(WITH ONE FIGURE)

At Thompson's Mills, northern Georgia, during the season of 1909, the writer's attention was called to an exceedingly interesting modification in one of the involucral bracts of upland cotton. This is shown natural size in the accompanying photograph. A portion of this particular member of the involucre retains the usual features of a normal bract, while the rest has become a typical leaf in shape. A more perfect combination of bract and leaf could hardly be expected. The bractlike portion appears to replace a single lobe of the leaf.

Aberrant variations of this nature are not readily explained. The earlier morphologists were wont to regard them too seriously as reversionary variations which really brought to light particular features of ancient progenitors. In many instances it would appear that considerable skill obtained in the invention of fanciful conceptions of evolutionary developments. Modern botanists, however, do not find it quite as convenient to explain many variations in this way.

The involucral bracts of cotton may have originated from typical foliage leaves which have become reduced by evolutionary processes, but the best of our evidence is exceedingly incomplete. The modification here shown is an interesting fact of variation, but whether or not it expresses any fact of evolutionary significance can be only roughly surmised. Any study of plants or animals reveals striking variations in all characters, and many are as incomprehensible in their origin or significance as life itself. Irregular variations, however, deserve to be carefully preserved. Although, taken singly, they may not appear very significant, large numbers may be more productive of significant conclusions.—H. A. ALLARD, *Bureau of Plant Industry, Department of Agriculture, Washington, D.C.*

THE BIOLOGICAL ANTAGONISM BETWEEN CALCIUM AND MAGNESIUM

In a recent number of the BOTANICAL GAZETTE (**49**:41–50. 1910), CHAS. B. LIPMAN stated that in regard to *Bacillus subtilis* an antagonism does not exist between calcium and magnesium. This fact is quite natural, however, since the microbes (with rare exceptions, as for example Azotobacter) do not require lime for their life and multiplication, and on the other hand an antagonism does not exist between those elements themselves, but merely between their functions. Magnesium salts, in the usual biological concentrations, cannot exert any poisonous action on lower fungi and algae, hence there is no need of any antagonistic element. These points have been extensively treated in a paper entitled "The physiological rôle of mineral nutrients in plants,"[1] to which the reader may be referred.—OSCAR LOEW, *Munich, Germany.*

[1] Bull. 45, Bur. Pl. Ind., U. S. Dept. Agric. 1903; especially on p. 44 and pp. 49–54.

CURRENT LITERATURE

BOOK REVIEWS

Vegetation in Belgium

One of the most important of ecological investigations is represented by the work of MASSART[1] along the Belgian coast and the neighboring alluvial lowlands. Perhaps no other similar work has been so detailed, and certainly no results of such a study have ever been presented in so sumptuous a form. For a decade and a half MASSART has carefully studied the restricted area here considered, and now there is presented a comprehensive monograph, though modestly entitled an essay. The first chapter deals with the past history of the region from the Miocene on. The modern (Holocene) period was initiated by the withdrawal of the sea and the formation of extensive peat deposits. Later came another invasion of the sea, Roman remains having been found beyond the present shore line. In the ninth century A.D. the Normans began a system of diking, which arrested the incursions of the sea and incited dune formation. At present there are extensive dune areas near the French border and also beyond Ostend and near the Dutch border. The alluvial deposits include chiefly the *polders*, fertile tracts within the dunes lying below sea-level and long ago reclaimed from the sea. Flat depressions among the dunes are known as *pannes* (perhaps to be translated into English as "pans"); an alluvial shore inundated at ordinary high tides is called a *slikke*, while the higher level inundated at the highest tides is called a *schorre*.

The second chapter, dealing with the conditions of plant existence, calls attention to the imperfections of ordinary meteorological data; for example, readings of ordinary air temperatures mean but little and should be replaced by readings of temperatures where the various plant organs, aerial and subterranean, are located; again it is shown how much more important are evaporation data than the more common humidity data. Various southern plants that cannot endure the winter at Brussels are uninjured on the coast. The influence of the winds on tree shape is very marked, and MASSART agrees with those who regard the influence of salt in causing deformity as insignificant when compared with desiccation; the trees most likely to be deformed are the silver poplar, linden, and elm. Very full tables

[1] MASSART, J., Essai de géographie botanique des districts littoraux et alluviaux de la Belgique, avec annexe contenant des listes de plantes, trente-deux planches doubles en phototypie, neuf planches de diagrammes et quatorze cartes. Recueil de l'Institut Botanique LÉO ERRERA **7**:167–584 + pp. 121. 1908.

BOMMER ET MASSART, Les aspects de la végétation en Belgique; I. MASSART, J., Les districts littoraux et alluviaux. *pls. 86*. Ministère de l'intérieur et de l'agriculture; Jardin botanique de l'état. Brussels. 1908.

are given, comparing the littoral climate of Belgium with that on other European coasts. By reason of mild temperatures, many plants retain green leaves through the winter, notably winter annuals, biennials, and many evergreen herbs. Other topics here treated are bud protection (RAUNKIAER'S classification being followed), fixation of dunes by vegetation (mosses and lichens being of great importance in this), reactions to the deposit and denudation of sand (e.g., ascent or descent of rhizomes), rigidity of the aerial organs, "adaptations" against desiccation. Consideration is next given to the soil, many analyses being presented, and to the influence of animals and of other plants upon the vegetation. Some attention is devoted to succession, as on the dunes, where Erodium often appears on a fresh surface, giving way later to *Festuca rubra*, and this to Tortula, and this again to various herbs, the succession culminating in a stand of *Salix repens*.

The third chapter has to do with the plant associations (the term formation being discarded). An association is defined as "l'ensemble des espèces végétales qui sont adaptées aux mêmes conditions d'existence et qui vivent donc en mélange dans une station, c'est-à-dire dans l'endroit où ces conditions d'existence sont réalisées." After considering the conditions obtaining on the littoral dunes, MASSART takes up the detailed features of the mobile and fixed dunes, the dry and wet "pans," winter pools and permanent pools, cultivated lands and forest plantations. The marine and fluvial alluvia are next considered, attention being given to the tidal belts (*slikke* and *schorre*), ditches, mounds, *polders*, brackish and fresh waters, ponds, canals, dikes, and cultivated areas. Finally there are treated the plants of the Cardium sands.

A chapter is devoted to a floristic comparison between the littoral and alluvial districts and other neighboring districts, Belgium being regarded as divided into two main regions, the domain of the plains and the domain of the hills and mountains. The final chapter deals with the origin of the flora. In the region considered there is not a single endemic species. The dune flora is dominantly "calcicole," thus differing from the dune floras of Holland, Denmark, and Germany. The Cardium sands, on the other hand, are tenanted mainly by "calcifuges."

The *Annexe* is devoted in part to a detailed list of plants, with data arranged in columns showing distribution in Belgium and elsewhere in Europe, and also giving the characteristic vegetative features of the plants considered, a unique and most suggestive kind of tabulation. Most of the *Annexe*, however, is filled with photographic reproductions of the various habitats, diagrams, and maps. The work on "Aspects de la végétation" (following out a plan elaborated by BOMMER in 1903) presents the same or similar photographs in most sumptuous form, the plates having the unusual size of 30×40^{cm}. Doubtless these are the most excellent ecological photographs that have ever been taken, and they are also issued in the most perfect form of any that have yet appeared. Indeed the entire monograph, including the detailed text with its many tables of climatic and edaphic data and vegetative features, as well as the numerous illustrations, may serve as one of the best models now extant for future ecological workers. Many of our

American ecologists who issue several papers a year, giving the results of a few days or weeks of study, may well follow the example of MASSART, who has minutely studied his restricted Belgian littoral in every season for fifteen years and more.—H. C. COWLES.

A new manual of Rocky Mountain botany

To those familiar with the *Manual of the botany of the Rocky Mountain region* which has been the standard field book for that section of the country for practically a quarter of a century, the appearance of a revised edition[2] will appeal with special interest. The territory covered by the present volume remains essentially the same as in the original edition, namely the Rocky Mountain region from Montana and southern Idaho to northern New Mexico and Arizona.

The text in the new edition has been entirely recast; the arrangement of families has been brought into the sequence of ENGLER and PRANTL; the descriptions of the older species in many cases have been rewritten in the light of more complete material and printed in uniform type; the results of taxonomic researches made on the flora of the region during recent years have been incorporated with few exceptions, thus bringing the manual to date; concise and well-contrasting keys have been placed at the beginning of all the larger genera; bibliographical reference is made to the original publication of species and varieties recognized; and limited synonomy is given, particularly wherever a change of name or new combination has been made. These are the salient features which characterize the revised edition.

The circumscription of families continues unchanged; and it is a pleasure to see such natural groups as Leguminosae and Compositae remain intact. The most striking contrast, however, when compared critically with the first edition, is in the matter of generic limitations. Here the reviser has had a difficult task, because of the very great botanical activity in exploration and taxonomic publication in recent years and the tendency toward segregation. Thus the effort to bring together in perfect harmony and to bestow proper value on all genera and species that have been proposed during the past twenty years from the Rocky Mountain region alone has been no light undertaking. And to be absolutely consistent would require essentially a monographic knowledge of every group represented within the limits of the flora. The taxonomist, therefore, may find himself at variance with the treatment of certain groups as delineated in the text. For example, Batrachium, Ranunculus, Halerpestes, Onagra, Anogra, Pachylophus, Lavauxia, Gaurella, Galpinsia, Meriolix, and Taraxia receive equal generic recognition; while other recently segregated groups like Saxifraga, Astragalus, Euphorbia, and Mentzelia have been retained in their broader sense, as they are

[2] COULTER, JOHN M., New manual of botany of the Central Rocky Mountains (vascular plants), revised by AVEN NELSON. 8vo. pp. 646. New York, Cincinnati, and Chicago: American Book Co. Actual date of publication, December 22, 1909.

usually defined. Hence in the treatment of genera a somewhat intermediate course has been followed.

In the interpretation and definition of species the work is conservative; in fact many of the recently proposed Rocky Mountain species have been reduced to synonomy. All categories subordinate to the species are treated uniformly under the trinomial, without further indication as to the supposed relationship to species; and it is only in the summary that we learn incidentally these are all regarded as varieties. The flora contains according to the summary given 116 families, 649 genera, 2733 species, and 186 varieties. This is by no means an excessive number for such a diversified region. A "list of new names and combinations" is also appended, which totals 169. Some of these combinations seem scarcely justifiable; for example, "*Krigia virginica* (L.) A. Nels." This is a name taken up for *K. amplexicaulis* Nutt. apparently on the basis of absolute priority, but which is in direct violation of section 7, article 53, of the International Rules of Botanical Nomenclature. A very complete and convenient index, including scientific and common names, arranged similar to that of the seventh edition of GRAY'S *Manual*, concludes the volume.

The press work is excellent, and there are comparatively few typographical errors. On page 529, under *Erigeron ramosus*, the date of publication for the *Preliminary catalogue*, etc., is given as "1788," a mere typographical error for 1888. On the whole the revised edition gives a concise, reasonably complete, inexpensive, and in general conservative treatise on the flora of a region which is always fascinating to the naturalist; and the clear-cut keys, and brief and lucid descriptions render the book particularly well adapted for the field identification of species. The botanical public is to be congratulated on having the revision of this well-known manual made by one whose continued activities in the field and extended knowledge of the Rocky Mountain flora have peculiarly fitted him for the work in hand.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Bot. **4**:593–600. 1909) under the title "Notes on Philippine orchids with descriptions of new species I" gives critical notes on several known orchidaceous plants and describes 3 species hitherto unknown.—O. BECCARI (*ibid.* 601–639. *pls. 30, 31*) has published, as new, 20 species and 7 varieties of Philippine palms.—W. BECKER (Beih. Bot. Centralbl. **26**:1–44. 1909) has issued the first of a series of articles on the taxonomy of European violets.—A. CHEVALIER (Journ. Bot. **22**:112–128. 1909) under the title "Diagnoses plantarum Africae" has published several new species of flowering plants, including a new genus (*Leocus*) of the Labiatae.—H. CHRIST (Journ. Linn. Soc. **39**:213–215. 1909) describes new species of ferns, 2 of which are from the Philippines.—C. CHRISTENSEN (Bot. Tidsskr. **29**:291–304. *figs. 15*. 1909) has published a new genus (*Stigmatopteris*) of ferns, based on *Polypodium flavopunctatum* Kaulf. (*Aspidium rotundatum* Willd.) and refers thereto 12 species from tropical America.—W. W. EGGLESTON (Bull. Torr. Bot.

Club **36**:639–642. 1909) describes 3 new species of North American Crataegi.—F. EICHLAM (Monats. Kakteenk. **19**:177–180. 1909) has described a new species of Cereus (*C. lepidanthus*) from Guatemala.—A. D. E. ELMER (Leafl. Philip. Bot. **2**:631, 632. 1909) proposes a new species of Grewia (*G. negrosensis*) from the Philippine Islands.—A. J. EWART, J. WHITE, and B. REES (Proc. Roy. Soc. Victoria **22**:6–23. *pls. 3–10.* 1909) under "Contributions to the flora of Australia, no. 11," have published several new species, referred to different genera, and include a new genus (*Gilruthia*) of the Compositae.—C. FERDINANDSEN and O. WINGE (Bot. Tidsskr. **29**:317–319. *figs. 6–8.* 1909) have published 3 new American species of fungi.—M. GANDOGER (Bull. Soc. Bot. Fr. IV. **9**:458–464. 1909) under the title "Les Anthurium de l'Ecuador" gives a conspectus of the known Ecuadorian species and publishes one species new to science.—R. R. GATES (Rep. Mo. Bot. Gard. **20**:123–137. 1909) presents a very useful analytical key to some of the segregates of Oenothera; the key is supplemented by a bibliography and descriptive notes.—D. GRIFFITHS (*ibid.* 81–95. *pls. 2–13*) under "Illustrated studies in the genus Opuntia II" describes 11 new species from southwestern United States.—L. S. GIBBS (Journ. Linn. Soc. **39**:130–212. *pls. 11–16.* 1909) in cooperation with several specialists contributes an important article on the montane flora of the Fiji Archipelago; the paper includes a number of species new to science.—E. L. GREENE (Muhlenbergia **6**:1–3. 1910) has described 3 new species of Eriogonum from southwestern United States.—A. E. GROBÉTY (Bull. Soc. Bot. Genève II. **1**:357, 358. 1909) proposes a new genus (*Ourococcus*) of the green algae, based on *Dactylococcus bicaudatus* A. Braun.—E. HACKEL (Rep. Nov. Sp. **7**:311–327. 1909) under the title "Gramineae novae VI" has published 17 new species of grasses, chiefly from South America; one genus (*Schizachne*) is new to science.—E. HACKEL and E. HASSLER (*ibid.* 369–383) under the title "Ex herbario Hassleriano: Novitates paraguariensis III" have described new species and varieties in the Gramineae, Rosaceae, and Malvaceae.—T. HERZOG (*ibid.* 354–359), supplementing a recent article on new siphonogamous plants from Bolivia, has published 6 additional species; the same author (Beih. Bot. Centralbl. **26**:45–102. *pls. 1–3.* 1909) has published 73 new species of mosses from Bolivia, and proposes three new genera (*Polymerodon*, *Simplicidens*, and *Wollnya*).—A. A. HELLER (Muhlenbergia **5**:145–153. *pls. 4, 5.* 1909) presents a second article on the "Nevada lupines," including a description and illustration of one new species.—A. W. HILL (Journ. Linn. Soc. **39**:216–230. 1909) gives a synopsis of the "Acaulescent species of Malvastrum," recognizing 18 species of which 5 from South America are new to science.—E. JANCHEN (Mitt. Naturwis. Ver. Univ. Wien **7**:1–124. 1909) has published a monographic treatment of the Cistaceae of Austria-Hungary, recognizing four genera, as follows: Cistus (4 species), Tuberaria (1 species), Helianthemum (11 species), and Fumana (5 species); bibliography and synonomy are given in detail.—M. E. JONES (Contr. West. Bot. no. 13. pp. 1–16. 1910) under the heading "New species and notes" characterizes 15 new species and 9 new varieties of flowering plants from western United States.—C. H. KAUFMAN (Rep. Mich. Acad. Sci. **11**:55–91. *figs. 3.* 1909)

records a list of fungi new to the state and gives a mongraphic treatment of the Michigan representation of Russula, in which 56 species are recognized, 5 being described as new to science.—N. C. KINDBERG (Ottawa Nat. **23**:180–191. 1910) in continuation of his studies on Canadian bryology records several species of mosses, as either new or noteworthy, from Canada.—M. BOULY DE LESDAIN (Bull. Soc. Bot. Fr. IV. **9**:473–477. 1909) has published 8 new species of lichens from Mexico and Peru.—G. MASSEE (Kew Bull. 1–6. *figs. 21.* 1910) has published several new species of fungi, 7 being from the West Indies. A new genus (*Hartiella*) of the Hyphomycetaceae is described from Trinidad; the fungus is parasitic on shells of the cacao pod.—E. D. MERRILL (Phil. Journ. Sci. Bot. **4**:641–650. 1909) has published a "Preliminary revision of Philippine Combretaceae," in which he recognizes four genera represented by 18 species; one new species of Terminalia is described.—W. A. MURRILL (Mycologia **2**:25, 26. 1910) describes a new phalloid genus (*Protophallus*) from Jamaica.—A. PASCHER (Ber. Deutsch. Bot. Gesell. **27**:555–562. *pl. 20.* 1909) describes and illustrates a new genus (*Pyramidochrysis*) of the Chromulinaceae; two species are recorded; both are found in stagnant water near Mugrau in southern Bohemia.—L. QUEHL (Monats. Kakteenk. **19**:188–189. 1909) describes a new species of Mamillaria (*M. pseudoperbella*) from Mexico.—A. REHDER (Rhodora **12**:1–3. 1910) records several noteworthy forms of *Kalmia latifolia*.—H. REHM (Ann. Mycol. **7**:524–542. 1909) has published several new species of Ascomycetes, 13 being from North America and 20 from South America; two new Brazilian genera are proposed, namely *Dictyomollisia* and *Phaeofabraea*.—J. F. ROCK (Bull. Torr. Bot. Club **36**:645, 646. 1909) describes and illustrates a new species of Scaveola from the Hawaiian Islands.—R. ROLAND-GOSSELIN (Rev. Hort. Paris **82**:28, 29. *fig. 8.* 1910) has published a new species of Cereus (*C. tricostatus*) which has been introduced into cultivation from Mexico.—R. A. ROLFE (Kew Bull. 364–368. 1909) has published several new species of orchids, of which 4 are from South America.—J. N. ROSE and J. A. PURPUS (Contr. U. S. Nat. Herb. **13**:45, 46. *pls. 10–14.* 1910) have described 3 new species of Echeveria from Mexico.—E. ROSENSTOCK (Rep. Nov. Sp. **7**:289–310. 1909) has published 38 new species and varieties of ferns. These species are based on collections made by Mr. R. SPRUCE in the region of the Amazon, in eastern Peru, and in Ecuador.—P. A. RYDBERG (Bull. Torr. Bot. Club **36**:675–698. 1909) under "Studies on the Rocky Mountain flora XX" has described several new species of sympetalous plants.—F. GRAF VON SCHWERIN (Mitt. Deutsch. Dendr. Gesell. 1–56. 1909) presents a monograph of the genus Sambucus, in which 21 species and numerous varieties are recognized; the text is accompanied by numerous illustrations and distribution-maps.—T. A. SPRAGUE (Kew Bull. 362–364. 1909) gives a synopsis of the American species of Microtropis, recognizing 5 species from Mexico and Central America, 2 being new to science.—F. THEISEN (Broteria Bot. Ser. **8**:53–65. *pls. 1–6.* 1909) under the title "Marasmii austro-brasilienses" enumerates 38 species of Marasmium, including 2 new species and 8 new varieties.—E. A. WAINIO (Phil. Journ. Sci. Bot. **4**:651–662. 1909) under the heading "Lichenes insularum philippi-

narum I" records 10 species and several varieties as new to science.—F. A. WOLF (Mycologia **2**:19–22. *pl. 18.* 1901) has published a new species of Fusarium, parasitic on *Viola tricolor*.—H. WOLFF (Rep. Nov. Sp. **7**:345, 346. 1909) has published a new species of Eryngium (*E. affine*) from Costa Rica.—C. H. WRIGHT (Kew Bull. 24. 1910) describes a new species of Urceocharis from Peru.—Different authors (*ibid.* 357–362. 1909) under the heading "Decades kewensis LIV" have published a number of new species of flowering plants, including a new genus (*Micholtzia*) of the Asclepiadaceae from India; also a new genus (*Ennealophus*) of the Iridaceae from Brazil.—J. M. GREENMAN.

A new genus of chytrids.—A minute organism parasitic in the leaf blades and petioles of the ragweed (*Ambrosia artemisiaefolia*) is described by GRIGGS[3] as a new genus. The swarm spores perforate the cell wall and enter the cells (epidermal, hypodermal, or chlorenchymal), sometimes in large numbers, where they present amoeboid forms within the plasma of the host. Some of the "amoebulae" unite in pairs by the fusion of their plasma while the nuclei remain distinct. This minute amoeboid zygote grows to form a binucleate resting spore which at maturity is provided with a stout exospore wall. The germination has not been studied. Other swarm spores, in the same or other cells, grow to form zoosporangia about 70 μ in diameter, showing also amoeboid movements in the vegetative stage. The nucleus of the young "amoebula" which is to form a zoosporangium is said to "fragment" into four nuclei at an early stage. Since the figure given presents just as much evidence that the four nuclei are derived by mitotic division as by fragmentation, it would be interesting to know if this is the period of meiosis. A rather extended period then follows before further successive division of these four nuclei to form the zoospores, which are 2.5 μ. The author saw no mitotic figures, but states that in some cases at least there is evidence that the nuclei fragment. The formation and escape of the zoospores was not observed, and he does not know whether the zoospores are ciliate or amoeboid, the latter he thinks more likely. Since the escape of the zoospores was not observed, he does not know whether or not an exit tube is formed from the sporangium. The species, which he names *M. stevensianum*, is associated with *Rhodochytrium spilanthides*, and while the infected cells increase greatly in size, very little deformity of the host occurs, although large numbers of cells in a limited area are affected.

Some of the speculations appear to be based on a misinterpretation of some statements of the reviewer in regard to the behavior of the zoospores of Rhizophidium, for he says: "ATKINSON has shown that when liberated inside the sporangium the zoospores swim actively forward until they strike the wall of the sporangium, when the flagella are retracted and the zoospore puts out pseudopodia by which it gropes for the opening of the sporangium. In case it is located too far from the ostiole to reach it with its pseudopodia, it resumes its flagellate form and

[3] GRIGGS, R. F., Monochytrium, a new genus of the Chytridiales, its life history and cytology. Ohio Nat. **10**:44–54. *pls. 3, 4.* 1910.

swims about again until it finally escapes." The reviewer did not state that the flagellum is retracted[4] when the amoeboid movements take place and does not regard it as at all likely that such is the case.

GRIGGS places the organism in the Olpideaceae, and states that it may be separated at once from all other genera of this family by its habitat. "All the other genera are parasites of aquatic plants or animals except Asterocystis, which infests the roots of the seed plants." He has probably overlooked certain species of Olpidium. *O. brassicae* (Wor.[5]) Dang.,[6] a typical Olpidium, is parasitic in the stems of cabbage seedlings. *O. simulans* (DeBary and Wor.[7]) Dang.[8] (see also A. FISCHER[9]) is parasitic in young leaves of *Taraxacum officinale* and is associated with *Synchytrium taraxaci*. SCHROETER[10] is inclined to believe this is a Pleolpidium, but it would still be a member of the Olpidiaceae. *Olpidium trifolii* (Pass.[11]) SCHROETER[12] on petioles and leaf blades of *Trifolium repens* is more doubtful; A. FISCHER[13] thinks it is a Synchytrium.

It is unfortunate that the author did not compare his organism with the genus *Reesia* Fisch[14] (pp. 8–17), since until we know more about the dehiscence of the zoosporangium and the form of the active zoospores, it would seem more reasonable to place it in this genus than to create a new one, largely hypothetical; for if the zoosporangia develop exit tubes and the zoospores are uniciliate, which is not unlikely, it would be a true Reesia.—GEO. F. ATKINSON.

Morphology of the grass flower.—SCHUSTER[15] has recently made extended investigations upon the structure and morphology of the flowers and spikelets of grasses. His results are based upon an examination of fresh and alcoholic

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[4] See BOT. GAZETTE **48**:321, 322, 324. 1909.

[5] *Chytridium brassicae* Woronin, M. (see pp. 556–558. *pl. 31. figs. 12–18*) in *Plasmodiophora brassicae*, Urheber der Kohlpflanzen-Hernie. Jahrb. Wiss. Bot. **11**:549–574. *pls. 29–34.* 1878.

[6] DANGEARD, P., Ann. Sci. Nat. Bot. VII. **4**:285, 327. 1886.

[7] *Chytridium* (*Olpidium*) *simulans* DeBary and Wor. (see p. 29. *pl. 2. figs. 11–16*), Beitrag zur Kenntniss der Chytridieen. Ber. Naturf. Ges. Freiburg **3**:Heft 2 (1–40 of separate). *pl. 1.* 1863.

[8] Rabenh., Krypt. Fl. Pilze **4**:29. 1892.

[9] ENGLER AND PRANTL, Pflanzenfam. **1**[1]:70. 1889.

[10] *Synchytrium trifolii* Pass. in Rab. Fung. Europ. 2419. 1877.

[11] COHN'S Krypt. Fl. Schles. Pilze **1**:181. 1889; and ENGLER und PRANTL, Pflanzenf. **1**[1]:68. 1889.

[12] Rabenh., Krypt. Fl. Pilze **4**:51. 1892.

[13] FISCH, CARL, Beitrag zur Kenntniss der Chytridiaceen. pp. 48. *pl. 1.* Erlangen. 1884.

[14] SCHUSTER, J., Ueber die Morphologie der Grasblüte. Flora **100**:213–266. *pls. 2–5. figs. 35.* 1910.

material, with special reference to the developmental history of the parts. By means of dissections and microtome sections of spikelets in various stages of growth, he arrives at what are represented to be definite conclusions concerning certain species in twenty-five genera. Among his results the following are of special interest:

From a phylogenetic standpoint he considers the grasses to have descended from lily-like plants in which there were six perianth divisions in two circles, six stamens, and a tricarpellate pistil. Among existing grass genera he places Streptochaeta as most primitive. In this genus there are three stigmas, six stamens, three inner and two outer organs which the author interprets as representing the inner perianth and the posterior segments of the outer perianth, all in the axil of the flowering glume or lemma. In the majority of grasses the floret, borne in the axil of the lemma, consists of a two-keeled palea, three stamens, two lodicules, and a pistil with a two-parted style. HACKEL and others have considered the palea to represent the prophyllum, an organ found at the base of a branch, between that and the main stem. SCHUSTER states, however, that the palea is formed by the union of the two posterior segments of the outer perianth circle of the primitive flower. The inner perianth circle is well developed in Streptochaeta, but is usually reduced to small organs, the lodicules, which commonly function as spreaders during anthesis. The swelling of the lodicules pries open the lemma, thus exposing the stamens and stigmas. Usually there are present only two lodicules, the posterior being absent, but in bamboos and some other grasses all three are present. In the more primitive forms, such as bamboos, there are six stamens, but in most grasses three are suppressed, while more rarely only one or two are present. He accounts for the numerous stamens of certain genera, such as Pariana and Luzuola, by the splitting up of the original six stamens. The pistil consists of three carpels, but the anterior carpel usually fails to produce a style branch.

Recently the morphology of the glumes of Elymus and Hordeum were investigated by SCHENCK,[15] who considered the glumes to be developed from lateral branches at the base of the spikelet. SCHUSTER controverts this, and states that the lower or outer glume originates as a single organ, but soon divides into two portions which stand side by side below the spikelet, the upper glume being suppressed. In certain species of Elymus, such as *E. arenarius*, the glumes are in nearly normal position, for which reason the author follows HOCHSTETTER[16] in separating this group under the genus name Leymus. The author further states that in the end spikelets of the spikes in Elymus and Hordeum, the glumes develop normally, that is, both are present and entire.

Concerning viviparous grasses, it was found that the bulblet-bearing character was more or less constantly inherited, but that by culture in a dry and nitrogen-poor substratum, these forms tended to revert to the normal seed-bearing state.—A. S. HITCHCOCK.

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[15] ENGLER'S Jahrb. **40**:97–113. 1907.

[16] Flora **31**:118. 1848.

Transpiration of evergreens.—PUGLISI[17] has recently published a long and detailed paper on the comparative transpiration of evergreen dicotyledons in winter, spring, and summer. He discusses *Laurus nobilis* L., *Laurus canariensis* Willd., *Persea indica* Spreng., *Persea gratissima* Gaertn., *Oreodaphne californica* Nees., *Cinnamomum Camphora* Nees. et Eberm., *Litsea* (*Tetranthera*) *japonica* Spreng. GARREAU'S method is used to determine the relative transpiration of the upper and the lower surface of the leaf, and the potometers of MOLL and of PFEFFER for observations on detached shoots, sometimes continued for a week.

The author's most important conclusions are: that the volatile oils present are highly efficient in preventing excessive transpiration; that the safeguards against an injurious amount of transpiration in the leaves studied do not prevent rapid transpiration when there is an adequate water supply from the roots; that the relative transpiration rate of the upper and lower leaf surfaces varies decidedly at different seasons; that transpiration varies with the season, having a winter minimum, a maximum at the beginning of spring, and a lowering to or nearly to the winter rate during the extreme heat and drought of summer.

The memoir is sufficiently important to merit attentive reading by everyone who is investigating similar problems. The results, however, should be scrutinized with care, since some of the values obtained by the potometer method are open to doubt. For example, in the losses per square decimeter of leaf surface obtained in the six sets of potometer measurements on transpiration of *Cinnamomum Camphora*, the values for the first day average nearly one and one-half times as large as those for the fourth day, of consecutive potometer readings for the same shoot. In the June readings for this species, the daily transpiration in grams per square decimeter with the MOLL potometer fell from 6^{gm} on the first day to 1.13^{gm} on the sixth day. Evidently some cause, perhaps the plugging of the vessels of the cut end of the shoot by bacteria, rendered the later observations valueless.

The author cites some of the best literature on the subject, but apparently has not seen VON GUTTENBERG'S most important paper.[18]—JOSEPH Y. BERGEN.

Mistletoe as a pest.—BRAY[19] has investigated the so-called mistletoe pest of the southwest, especially its destructive work in central Texas. It seems that the mistletoe is most destructive in the region of transition from a humid forest climate to a dry climate less favorable for trees, for it is in such a region that the light becomes more favorable for the parasite. The destruction is due in part to mechanical injury, but more especially to the drain on the water and nutritive supplies of the host, which is effected by the "sinkers" connecting the parasite

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[17] PUGLISI, M., Contribuzione allo studio della transpirazione nelle piante sempre verdi. Annali di Botanica **7**:517–652. *pl. 22.* 1909.

[18] GUTTENBERG, H. VON, Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Bot. Jahrb. **38**:383–444. *pls. 7–9.* 1907.

[19] BRAY, WILLIAM L., The mistletoe pest in the southwest. Bull. 166, Bur. Pl. Ind., U. S. Depart. Agric. pp. 39. *pls. 2. figs. 7.* 1910.

with the xylem vessels, and by the "cortical roots" that traverse the "soft bark." An interesting description is given of the behavior of these digesting roots ("sinkers") in penetrating tissue, and in sending out lateral outgrowths ("cortical roots") which spread extensively through the cortex of the host and in turn give rise to other "sinkers" that connect with the xylem. The first infection of a tree is brought about by birds, and the subsequent spread of the parasite is caused by the falling or washing of berries upon other parts of the host. The seed and seedling exhibit unusual resistance to desiccation, and so survive the more or less prolonged period of establishment, a period which may extend beyond the first growing season. A tree may become affected at any point where living tissue is exposed or covered only by a thin layer of cork with lenticels, but the most vulnerable points are the young branches, and sometimes the buds. Various suggestions are made as to the treatment of trees subject to the attacks of this parasite. —J. M. C.

Latex.—Miss DIANA BRUSCHI has made a study of the latex of five species of Euphorbia and three of Ficus,[20] in an endeavor to clear up in a measure the contradictory results of various investigators, of which the two most recent studies by MOLISCH (1901) and KNIEP (1905) are characteristic. Dr. BRUSCHI finds that the quantity of latex, its pressure, and its aspect vary with the season in the figs, *Ficus Carica* and *F. pseudocarica*, but not the euphorbias. Of the components of the latex the proteins vary in quantity with the season in the two figs named, in which they are abundant; but they are scant in *F. elastica* and the euphorbias. The fats are without doubt the most important plastic components and they clearly follow the variations in photosynthesis. The starch remains an enigma. Reducing sugars increase a little in *F. Carica* and *F. pseudocarica* but change little in the others. On the whole Miss BRUSCHI upholds MOLISCH'S view of the latex as a cell sap circulating in a living plasma sac, which is not entirely aplastic. Inasmuch as it contains many substances easily utilizable as foods, the utilization of these foods is correlated with the activation and activity of the related enzymes. The ready use of the fats is certain, and they are the principal if not the only plastic material; the indifference of the starch is supposed to be due to the lack of an amylase energetic enough to attack it. As the latex tubes run usually in the midst of organs well supplied with foods by photosynthesis, their content is yielded only when all other foods are exhausted.—C. R. B.

Rhizoids of liverworts.—WEINERT has investigated the growth and tropisms of the rhizoids of Marchantia and Lunularia.[21] He finds that light promotes the formation of rhizoids from gemmae, and is quite indispensable for the development of the divergent rhizoids of the thallus; further, only a few of the appressed

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[20] BRUSCHI, DIANA, Contributo allo studio fisiologico del latice. Annali di Botanica **7**:671–701. 1909.

[21] WEINERT, HANS, Untersuchungen über Wachstum und tropistische Bewegungserscheinungen der Rhizoiden thallöser Lebermoose. Bot. Zeit. **67**[1]:201–230. *figs. 11.* 1909.

sort, and these with poor pegs, are formed in darkness. Even if a thallus raised in darkness be afterward lighted, it forms no divergent rhizoids; and if such a thallus after being cut off regenerates itself, the new part forms none; the power once lost seems finally gone. Rhizoids cut off are not regenerated, but new ones are formed, either from surface cells of the thallus or from a cell internal to the first rhizoid-producing cell, in which case the new one grows through the old, as previously reported by KNY, DIXON, and others. WEINERT finds that small pegs occur even in true divergent rhizoids, which indicates to the reviewer that the possession of rhizoids of two kinds has been overvalued as a marchantiaceous character, for example in the case of Monoclea.

While the formation of rhizoids on the under side of gemmae is promoted by gravity, the hairs themselves are not geotropic, but are highly sensitive to light, being negatively phototropic even in weak red light, but strangely enough, not in blue light. The divergent rhizoids of the thallus are very slightly phototropic (negative). The appressed rhizoids show no tropisms.—C. R. B.

The origin of Oenothera gigas.—GATES[22] has investigated the relation of the number of chromosomes in *Oenothera gigas* to its size. This mutant from *O. Lamarckiana* has double the number of chromosomes (28) possessed by the parent form and by the other mutants examined. In every tissue examined, the cells of the mutant are conspicuously larger than those of the parent form, and the nuclei of the pollen mother cells during synapsis are about twice as large. The author suggests that increase in the size of nuclei and cells, consequent upon or coincident with the doubling of the chromosome number, and change in the relative dimensions of the cells in some cases, will account for all the differences between the two species. There is no evidence of the presence of new or additional unit characters in *O. gigas*. It is concluded that the facts strongly support the view of the independence and genetic continuity of the chromosomes, whatever may be their rôle in heredity. It is suggested as most probable that the double number of chromosomes in *O. gigas* originated soon after fertilization, by the failure of a nucleus to complete its division after the chromosomes had divided. This doubling of the number of chromosomes, the author thinks, "cannot be a common method of species formation, and bear no necessary relation to the general processes of evolution in the group." He speaks of it rather as an incident among evolutionary phenomena.—J. M. C.

Farm water supplies.—The Bureau of Plant Industry has been cooperating with the Minnesota State Board of Health in an investigation of the farm water supplies of that state, and a report by KELLERMAN and WHITTAKER has now been published.[23] Numerous cases and their details are presented, classified under

[22] GATES, REGINALD RUGGLES, The stature and chromosomes of *Oenothera gigas* DeVries. Archiv. für Zellforschung **3**:525–552. 1909.

[23] KELLERMAN, KARL F., AND WHITTAKER, H. A., Farm water supplies of Minnesota. Bull. 154, Bur. Pl. Ind., U. S. Depart. Agric. pp. 89. *figs.* 73. 1909.

the following headings: dug wells, bored wells, drilled wells, driven wells, springs, rivers, surface reservoirs, and cisterns. Some of the general conclusions are as follows: Both farm and city are suffering from the careless management of rural sanitation. Exhaustive data upon 79 carefully selected and representative rural water supplies show that 20 were good and 59 polluted, usually because of careless or ignorant management. Some of the polluted wells are so located that even extreme care would not make them safe, but a large majority of them could be made safe. The rivers, surface reservoirs, and cisterns are all polluted, and it is doubtful whether satisfactory supplies can be secured for farm use from such sources, except by disinfection. During the investigation 23 of the farms examined showed a record of typhoid fever. It is stated that "the protection of farm supplies by common-sense methods, obvious to anyone who will try to discover the dangers incident to his own water supply, would render safe the majority of the farm supplies which are now polluted."—J. M. C.

Ferments of resting seeds.—Miss WHITE[24] has shown that the enzymes present in seeds of wheat, maize, barley, oats, and rye retain their activity long after the power of germination of the seeds has disappeared. Diastatic and proteolytic enzymes were shown to be present in wheat after twenty years of storage, and in oats, rye, and barley after eight to ten years of storage, although the seeds had lost their power of germinating. The enzymes persisted apparently unaffected by the long period of storage. The resistance of the enzymes to heat was also tested. In a moist condition all the enzymes are destroyed at 100°, but in a dry state they can resist higher temperatures. Pepsin was destroyed in one hour at 124°, erepsin in one hour at 124°–128°, and diastase at 124°–131.° Both as to duration of time and effects of heat the enzymes are more persistent than the power of germination, showing that failure to germinate is not necessarily correlated with loss of enzymes. In the final part of the paper the respiratory activity of resting seeds is taken up. Many air-dried seeds give off appreciable quantities of carbon dioxid, but others show no respiration. When seeds are moderately desiccated at 45° all respiration ceases.—H. HASSELBRING.

Position of chloroplasts.—SENN's continued investigations[25] on some details of the position of chloroplasts offer opportunity to call attention to his independently published work,[26] which was not received by the GAZETTE. In his last contribution, after alluding to certain adverse criticisms on his former results, he reports investigations on the winter position of the chloroplasts in the palisade cells of winter-green foliage. He concludes that the heaping up of the

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[24] WHITE, Miss JEAN, The ferments and latent life of resting seeds. Proc. Roy. Soc. B **81**:417–442. 1909.

[25] SENN, G., Weitere Untersuchungen über die Gestalts- und Lageveränderung der Chromatophoren. Ber. Deutsch. Bot. Gesells. **27**:(12)–(27). 1909.

[26] ———, Die Gestalts- und Lageveränderung der Pflanzen-Chromatophoren. Leipzig: Wilhelm Engelmann. 1908.

chloroplasts in the bottom of the palisades is a local effect of the frost, which induces in the chloroplasts, and perhaps in the semifluid protoplasm also, a negative thermotactic migration.

SENN has also studied the migration of one of the chloroplasts of *Synedra Ulna* after division. The division of the diatom is of course longitudinal, while the two chromatophores divide transversely. One of each new pair, therefore, must move diagonally from one end of the old valve to the face of the new, elongating at the same time, while its fellow merely elongates to fill the old valve. The movement seems to be a true migration, not simultaneous in all parts of the chloroplast, but progressive while the elongation is going on.—C. R. B.

Coloring matter of tomato.—WILLSTÄTTER and ESCHER[27] have investigated the coloring matter of the tomato and come to the conclusion that it is a compound isomeric with carotin, but not identical with it as other investigators have claimed. The coloring matter, for which they retain SCHUNCK's name lycopin, was extracted from both fresh and preserved tomatoes. The yield from 135^{kg} fresh tomatoes was 2.7^{gm}, and from 74^{kg} preserved tomatoes 11^{gm}. The tomatoes are dried by repeated washing with alcohol, which is finally pressed out. The residue is further dried on a water bath, ground to powder, and extracted with carbon bisulfid, which is driven off under reduced pressure. After being washed with alcohol and petroleum ether, the raw lycopin was most advantageously recrystallized from gasoline. The empirical formula is C_5H_7, and the molecular formula $C_{40}H_{56}$ corresponds with carotin. Lycopin differs from carotin, however, in its crystal form and other physical properties, and in its chemical behavior toward oxygen and halogens. Both substances undergo auto-oxidation, but the quantities of oxygen absorbed differ in the two cases.—H. HASSELBRING.

Plant succession in Nova Scotia.—TRANSEAU[28] has outlined the succession of plant societies found on a portion of the southwestern coast of Nova Scotia. Several lines of physiographic succession have been investigated, and all are found to lead to the Picea formation, a forest association dominated by *Picea mariana* with a small percentage of *Abies balsamea* and *Picea canadensis*. The marine line of succession leads from the Laminaria and Fucus formations through a salt marsh with typical associations passing through an Alnus-Myrica shrub association to the final forest stage. The hydrophytic series has the same fate, the Sphagnum and Larix associations being two stages which usually precede the spruce. From the dry beach with Ammophila and Atriplex the transition is through the Alnus-Myrica association to the Picea forest. The final coniferous association varies considerably in density, but the trees are seldom more than 10^{m} high; geographically it belongs to the author's northeastern conifer forest center.—GEO. D. FULLER.

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[27] WILLSTÄTTER, R., AND ESCHER, H. H., Ueber den Farbstoff der Tomate. Zeit. Physiol. Chemie **64**:47–61. *pl. 1. figs. 1.* 1910.

[28] TRANSEAU, EDGAR N., Successional relations of the vegetation about Yarmouth, Nova Scotia. Plant World **12**:271–281. *figs. 4.* 1909.

Oxidase of Medicago.—EULER and BOLIN[29] claim to have succeeded in purifying and determining the chemical constitution of the oxidase (laccase) of Medicago. The purification was greatly furthered by the discovery that the substance was not sensitive to high temperatures. By boiling the extracted juice, the protein bodies were thrown down, and by treatment with animal charcoal, the dextrin-like substances withdrawn. They concluded that this pure laccase consists of mono-, di-, and tribasic aliphatic oxy-acids. The presence of the citrate, malate, and mesoxalate of this base was certainly established, and it is almost certain that the glycolate is a fourth salt.

They have already[30] shown that various salts of this type will produce oxidations qualitatively and quantitatively, similar to those produced by the laccase of Medicago. They now extend these tests to the new salts found, and to mixtures of the salts, and find marked agreement between the oxidations produced by them and those produced by laccase.—WILLIAM CROCKER.

Origin of the cell wall.—In an extended paper on vegetative cell division in the higher plants, POSTMA[31] pays particular attention to the origin and development of the cell wall. Half of the paper consists of an excellent presentation and discussion of the literature, while the writer's own researches deal with the stomata of *Aneimia fraxinifolia*, root tips of *Allium Cepa*, and stem tips of *Psilotum triquetrum*. In case of the peculiar, isolated stomata of Aneimia, the cell wall is formed as in other vegetative cells, and consequently the problem in the three forms is much the same. While the writer finds that the cell wall arises in greater or less connection with the spindle, the material of the spindle is not believed to furnish all the material for the beginning of the wall. A mother *Hautschicht* splitting into two daughter *Hautschichts*, as sometimes described, could not be found. A single plate with rather small figures is hardly sufficient to illustrate so difficult and so important a problem.—CHARLES J. CHAMBERLAIN.

Seedlings of monocotyledons.—EVANS[32] has undertaken a somewhat extensive study of monocotyledonous seedlings and also of the mature embryos. Not only has the structure at various stages been investigated, but also the effect of deep and shallow seed-sowing. The present paper is a record of some of the results, chiefly those in reference to the "plumular meristem"; and a final paper will review all the facts and suggest the conclusions. The facts are to be used, in part, in connection with the question as to the origin of the lateral position of

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[29] EULER, H., AND BOLIN, IVAN, Ueber die Reindarstellung und die chemische Konstitution einer Oxydase. Arkiv for Kemi, Mineralogi, och Geologi **3**:000. 1909.

[30] ———, Zeit. Physiol. Chem. **51**:80. 1908.

[31] POSTMA, G., Bigdrage tot de Kennis van de vegetatieve celdeling bij de hogere plants. Dissertation. pp. 117. *pl. 1*. Groningen: M. de Waal. 1909.

[32] EVANS, W. EDGAR, On the further development during germination of monocotylous embryos; with special reference to their plumular meristem. Notes Roy. Bot. Gard. Edinburg No. 21:1–21. *pls. 53, 54. figs. 8*. 1909.

monocotyledonous leaves, which involves the nature of the cotyledon and the origin of the stem. The arrangement of the material is in a series beginning with an illustration "in which the leaves always appear lateral, and ending with as extreme a case of stem suppression as possible." The genera presented in the present paper are Asparagus, Ruscus, Danae, Semele, Polygonatum, and Smilax. —J. M. C.

Physcia villosa from North America.—In the HASSE collection of lichens, recently purchased by the New York Botanic Gardens, I found included with the genus Evernia, and labelled *E. prunastri* (L.), a specimen of *Physcia villosa* (Ach.) Duby, collected in 1892 at the Santa Barbara Islands, California, by BLANCH TRASK. The specimen is fertile; the spores normal, bilocular, 5–6 by 13–16 μ. This is the first record for this plant in North America, so far as I am aware. The type came apparently from Peru. Through the kindness of DR. N. L. BRITTON the specimen was forwarded by MR. R. S. WILLIAMS to DR. HASSE, who writes me under date of February 25, 1910: "I have collected the same [plant] near Point Loma, near San Diego, California, and farther north near Newport, Orange Co.—R. HEBER HOWE, JR., *Thoreau Museum, Concord, Mass.*

The resting nucleus.—In discussing the structure of the resting nucleus ROSENBERG[33] pays particular attention to the occurrence of distinguishable chromosomes in the resting cells of various parts of plants of several families. These chromosomes, or "prochromosomes," the existence of which has been denied by some writers, he now identifies in about forty new cases, figuring the debatable structures in Nuphar, Helianthus, Atriplex, Lupinus, Pinguicula, and Drosera. The paper is an added argument for the theory of the individuality of the chromosome.—CHARLES J. CHAMBERLAIN.

Morphology of Geissoloma.—STEPHENS[34] has studied the embryo sac and embryo of *Geissoloma marginata*, a small shrub of southwestern South Africa, and representing a family (Geissolomaceae) closely related to Penaeaceae, whose genera he had investigated previously. It proved to be "normal" in these structures, showing none of the peculiarities of Penaeaceae. In general, the results showed an embryo sac derived from one of a row of megaspores, very evanescent antipodal cells, a pear-shaped (later spherical) proembryo, and no suspensor.—J. M. C.

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[33] ROSENBERG, O., Ueber den Bau der Ruhekerns. Svensk. Bot. Tidskrift **3**:163–173. *pl. 5.* 1909.

[34] STEPHENS, E. L., The embryo sac and embryo of *Geissoloma marginata*. New Phytol. **8**:345–348. *pl. 6.* 1909.